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Systematics and biogeography of the arctic and boreal species of *Primula*

Kelso, Sylvia, Ph.D.

University of Alaska Fairbanks, 1987

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SYSTEMATICS AND BIOGEOGRAPHY OF THE ARCTIC AND BOREAL SPECIES OF *PRIMULA*

A THESIS

Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By
Sylvia Kelso, B.A., M.A.

Fairbanks, Alaska
September 1987

SYSTEMATICS AND BIOGEOGRAPHY OF ARCTIC AND BOREAL SPECIES OF *PRIMULA*

RECOMMENDED:

W. Scott Armbruster

Gerald F. Shields

Leslie A. Viereck

S. F. Macleon Jr.

David D. Murphy

Chairman, Advisory Committee

Ronald L. Smith

Department Head (acting)

APPROVED:

Dean, College of Natural Sciences

W C Thomas

Director of Graduate Programs

15 June 1987

Date

ABSTRACT

Four sections of the genus *Primula* are represented in northern North America: *Aleuritia, Armerina , Crystallophlomis,* and *Cuneifolia.* In this dissertation I discuss anatomical, morphological, cytological, ecological, and reproductive characters for thirteen species, and demonstrate coherence of sectional groups through cluster analysis and ordination. In *Primula,* distyly and homostyly play critical roles in systematics and biogeography. It is generally assumed that distylous individuals are almost completely outcrossed, and homostyles are capable of selfing. In the taxa examined here, distyly exists at the diploid and tetraploid levels while homostyly is seen in both diploids and higher polyploids. I suggest that distyly breaks down with selection for reproductive assurance in environments where pollinators are unreliable, or following hybridization in conjunction with polyploidy. While most northern *Primula* species are homostylous, several examples of distylous taxa demonstrate that this can be a successful breeding system in higher latitudes. In homostyles, self-compatibility and the proximity of reproductive organs assures a high degree of selfing; however, most northern homostylous taxa also exhibit attributes which suggest facultative outcrossing is common. In North America, evolution in *Primula* has been strongly influenced by Quaternary events leading to isolation, migration, and secondary contact of gene pools, in association with the breakdown of distyly to homostyly. The success of homostylous taxa is at least partially due to their ability to self-fertilize coupled with the availability of areas to colonize when Pleistocene ice retreated. The phytogeographic affinities, cytology, and reproductive shifts of *Primula* make it a useful model for processes occurring in the Alaskan flora. The steppes and mountains of Asia have been important source areas, and migration has taken place along mountains, rivers, island arcs, and coastlines. Speciation in the genus has been aided by hybridization, polyploidy, and reproductive diversity.

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Introduction

The large genus *Primula* L. is widely distributed throughout the north temperate latitudes of Eurasia and North America. It is also represented in the Arctic, and there is one disjunct species found at the southern tip of South America. Of the ca 500 species now recognized, the majority are found in the mountainous regions of Asia, particularly northwestern China and the Himalayan massif. While there are a few widespread circumboreal or Eurasiatic taxa, most have relatively restricted ranges. Certain geographic regions (e.g., the European Alps) and certain sections of the genus (e.g., section *Parryi* of western North America) are remarkable for the number of narrowly endemic species that they contain.

Within the Primulaceae, there are several genera closely related to *Primula.* In some cases these can be separated only by a combination of characters (Wendelbo 1961b, 1966). The genus *Androsace* L., with its segregates *Douglasia* Lindley and *Vitaliana* Sesler, and the genus *Dionysia* Fenzl are generally regarded as being the closest relatives of *Primula.* In some floras (e.g., Federov 1952) some mono- or bitypic genera including *Omphalogramma* Franchet, *Sredinskaya* (Stein) Fed., and *Kaufmannia* Rgl. are recognized as distinct from *Primula.*

The genus *Dionysia* grows in the mountains of Iran and Afghanistan. Wendelbo (1961a) separates it from *Primula* by its suffrutescent habit, marcescent leaves, longer exannulate corolla tube, shorter capsules, and stephanocolpate pollen. Certain species in *Primula* section *Sphondylia* Duby may show one or more of these attributes, but together, they effectively distinguish *Dionysia* from all other genera in the Primulaceae.

The genus *Androsace,* distributed throughout alpine regions of the northern hemisphere, is separated from *Primula* by its consistent homostyly, its shorter and constricted corolla tube, linear leaves, and porate rather than colpate pollen. The related genus *Douglasia* contains six species which are all narrow alpine endemics in northwestern North America and northeastern Asia. *Androsace* and *Douglasia* are treated as distinct in all contemporary North American floras; however, their relationship in North America has not been examined closely by a systematist in recent years. There are some indications that *Douglasia* may not be consistently separable from *Androsace.* (cf. Constance 1938; Wendelbo 1961c), and

Wendelbo (1961) has suggested that it might be more properly regarded as a subgenus of *Androsace.*

Early monographic treatments of the genus *Primula* were done by Lehmann (1817), Duby (1844), Pax (1889), and Pax and Knuth (1905). Smith and Fletcher (1941, 1942a, 1942b, 1942c, 1943, 1944a, 1944b, 1946, 1948a, 1948b, 1949) were the most recent monographers. They inspired a number of intrepid collectors to visit remote areas in Asia and bring back specimens to Edinburgh where the *Primula* beds at the Royal Botanical Garden were world famous. These gardens and the herbarium collections there remain one of the largest sources of *Primula* material. Although based on traditional morphological interpretations of taxa and limited material of some species (particularly North American ones), the work of Smith and Fletcher stands as the most comprehensive taxonomic treatment of the genus to date.

The initial sectional arrangement of *Primula* was created by Duby (1844). His sections were based, as were all such arrangements of the time, on simple external morphology without regard to the more phylogenetically important characteristics of cytology, anatomy, or chemistry that are seen as essential in contemporary systematics. This early sectional nomenclature received some revision by Balfour (1913), who had a perspective on many Asiatic taxa that were not known to Duby, by Bruun (1932) who worked on the cytology of the genus, and by Smith and Forrest (1928). A more recent system of sectional classification in *Primula* is that of Wendelbo (1961b) who synthesized features of previous classifications and incorporated some contemporary knowledge of cytology and anatomy into his arrangement. Additional modifications to the system of Wendelbo were added by Schwarz (1968). The nomenclature of Wendelbo and Schwarz was adopted by Tutin et al. (1972) for the *Flora Europaea* project, with some modification, by Tolmatchev and Yurtsev (1980) for the Primulas of the arctic USSR, and by Fenderson (1986) in his synopsis of the genus.

No attention has been given to an examination of North American Primulas on a comprehensive basis. Fernald (1928) revised section *Farinosae* (now called section *Aleuritia)* and Williams (1936) provided a brief overview of the genus in western North America. Since these papers were published, several new taxa have been described, our appreciation of others has been modified, and much more has

been learned about the biogeography of the genus in North America. It is also clear that modern systematic approaches such as cytology and reproductive ecology can provide new insights into the genus.

This dissertation provides a comprehensive taxonomic and biogeographic treatment of four sections of *Primula* in North America: section *Aleuritia* Duby, section *Armerina* Lindl., section *Crystallophlomis* Rupr., and section *Cuneifolia* Balfour. The primary focus is on the taxa found in Alaska. There is a fifth section of the genus represented in North America, section *Parryi* Smith, but its members are found solely in the western cordillera and are not treated here. With one exception, sectional nomenclature follows that of Wendelbo (1961b), Schwarz (1968), and Fenderson (1986). As explained in the text, I do not agree with the subsectional designations within section *Armerina,* and therefore I do not follow Schwarz in applying the names subsect. *Armerina* and subsect. *Chamaecome.* The generic and sectional descriptions used follow Fenderson (1986), with the exception of the cytological information which I have added on the basis of my own research. The species descriptions are based on my own observations.

The purposes of this study are as follows:

1. To determine the characters that are taxonomically and evolutionarily important in *Primula*..
2. To provide complete taxonomic descriptions of the arctic and boreal species of *Primula.*
3. To provide biogeographic descriptions of the arctic/boreal species with a focus on how contemporary and historical factors have affected these distributions.
4. To provide a tentative phylogenetic history of the northern *Primula* species.
5. To use this detailed generic analysis to provide insights into the origin of the Alaskan flora.

Materials and Methods

Field studies.

Field studies on *Primula* were carried out in Alaska at numerous locations from the Seward Peninsula, the Alaska Range around Denali National Park, along the Tanana River in Fairbanks, the Delta River near Donnelly Creek, and the Northway region along the upper Tanana. In the southwest Yukon, populations were studied along the Donjek River, near the confluence of the White and Koidern Rivers, and from the southern tip of Kluane Lake. In addition, live material from the Arctic Coastal Plain, St. Matthew Island, the Kuskokwim Mountains, and Cordova was cultivated in outdoor gardens in Fairbanks. Ecological descriptions for the Alaskan species follow the vegetation classification given in Viereck et al. (1986).

Herbarium.

Approximately 1600 herbarium specimens were examined to determine morphological characteristics of the taxa over their entire range. These specimens represented material from ALA, ALTA, BM, BRY, CAN, CAS, COLO, DAO, E, GH, ID, ISC, K, NDG, NY, PH, RSA, S, T, UBC, UPS, US, UTC, and WTU. Measurements were made on representative specimens of each taxon.

Cytology.

Mitotic chromosome numbers were obtained from root tips, and meiotic numbers from young anthers. Seeds were stratified on damp filter paper at 5°-8° C for 4 weeks, then germinated under alternating conditions of light and dark at temperatures of 15° and 8° respectively. Root tips were pretreated in a .002 M solution of 8-hydroxyquinoline for 2-3 hours at 10°, then fixed in a 3:1 solution of 95% ethanol: glacial acetic acid. The same protocol of pretreatment and fixation was followed for meiotic material. Chromosomes were stained with leucobasic fuchsin dye following the Feulgen procedure given in Darlington and LaCoeur (1975). Counts were made using a Wilde M20 compound microscope. Voucher herbarium material and slides are at the University of Alaska Herbarium (ALA).

Anatomy.

Live material was preserved in FAA solution (equal parts formalin: glacial acetic acid: 95% ethanol). Permanent slides of gland anatomy were prepared by

excising calyx lobes and mounting them in Hoyer's Medium (Bowers 1964). Taxa for which live material was not available were documented by excising a calyx lobe from an herbarium specimen, wetting it in FAA, and mounting in Hoyer's Medium. Material was photographed through a Wilde M20 trinocular microscope. Pollen was obtained from either undehisced anthers of preserved material or herbarium specimens. When herbarium specimens were used, the anthers were soaked in FAA for 24 hours before pollen was removed in order to standardize any effects of swelling. Pollen from both preserved material and herbarium specimens was mounted in Hoyer's Medium, and measured with an ocular micrometer in a Wilde M20 compound microscope.

Scanning Electron Microscopy.

Pollen, seeds, and stigmatic surfaces were examined with a JEOL JSM-35U scanning electron microscope (SEM). For stigmatic morphology, flowers were collected in the field and preserved in FAA. Stigmas were excised and put through an ethanol series for dehydration: 70%, 95%, 100%, 100%. They were critical point dried with carbon dioxide in a Bomar 100 critical point dryer, then mounted on aluminum stubs. Specimens were sputter-coated with gold or gold/palladium to a depth of 450 Angstroms on an SPI sputter coater. Pollen from either undehisced anthers of preserved material or herbarium specimens was mounted, air-dried, and coated as described above. Seeds were air-dried without ethanol dehydration, then mounted and coated as described above.

Numerical Methods.

Descriptive statistics, cluster analyses, and principal coordinates analysis were all done on a DEC Vax 8800 computer with SPSSX v. 2.2. Gower Similarity Coefficients were calculated with the program MIXSIM (Zurcher 1982) and cladograms with the program PHYLIP (Felstenstein 1984). Cophenetic correlation coefficients, regressions, and other plots were calculated and drawn with the packages Statview 512+ (Brainpower, Inc. 1986) and Cricket Graph (Cricket Software 1985) on a MacIntosh Plus microcomputer.

Chapter One
Taxonomic Characters in *Primula*.

Although large and geographically widespread, the genus *Primula* is uniformly conservative in its morphology. Few of its ca 500 species depart from the basic organization of an umbel of tubular zygomorphic flowers with a basal rosette of leaves. Because of this lack of phenotypic diversity, the genus is considered taxonomically difficult. Species of *Primula,* and likewise genera in the Primulaceae, are often distinguished only by a combination of characters rather than by a single attribute. These diagnostic attributes can change dramatically with ontogeny. For example, height of the scape can increase six-fold during the blooming period, farina that is dense on young leaves almost disappears on fruiting specimens, pedicels that are capillary at anthesis stiffen and become erect as capsules ripen. Furthermore, *Primula* species often are phenotypically plastic in their vegetative and reproductive responses to environmental conditions. However, in spite of the need to give most of the northern *Primula* species a generous morphological amplitude, all taxa show a coherent and identifiable phenotype when the effects of phenology and environment are taken into account.

There are two other factors critical to understanding the overall morphology of North American Primulas: the role of polyploidy and the role of the breeding system in the evolution of the taxa. Polyploidy has been a major force in the diversification of *Primula* section *Aleuritia.* With respect to morphology, it is important for two reasons. First, this section contains a number of closely related allopolyploid taxa. They are the products of reticulate evolution and the higher polyploid taxa strongly resemble each other. Second, it has been documented in many other genera that polyploidy can have distinct morphological and anatomical side effects. Increase in size of cells or organs is common, and many of the size-related characters discussed below can probably be attributed to polyploidy, at least within section *Aleuritia.*

In the four sections of *Primula* treated here, there are both distylous and

homostylous taxa. Because of their clear genetic basis, distyly and homostyly can have important taxonomic implications, not only in themselves, but also because they affect whether the reproductive mode is outcrossing or self-fertilizing. Distylous taxa have two morphs that differ from one another in a number of ways, including the reciprocal placement of androecium and gynoecium. Most importantly, a strong intramorph incompatibility system almost completely insures obligate outcrossing within a population. In comparison, homostylous morphs represent a derived condition in which a single mutation has resulted in the combination of intermorph male and female organs. A homostyle is thus self-fertile, and due to the proximity of stigma and anthers, is believed to have high selfing rates. Ornduff (1969) has discussed how xenogamy and autogamy can have morphological and consequently, taxonomic implications. In *Primula* many of the morphological characters that are strong species markers may be a function of the breeding system, which in turn is a function of distyly or homostyly. This topic is discussed in detail in Chapter 4.

I. Cytological characters

The only effort at a comprehensive treatment of the cytology of the genus *Primula* was done by Bruun (1930, 1932). Sophisticated cytological techniques were not yet available to Bruun who made a pioneer effort to link cytology and systematics. A considerable portion of his paper was devoted to a justification of chromosome botany and discussion of what karyology can offer phylogenetic reconstructions. There are numerous chromosome counts given in the paper, and many of these have since been verified by other documented counts. Unfortunately, however, Bruun did not give voucher specimens for his chromosome numbers, and it is impossible to resolve those counts that show discrepancy with recent numbers.

The work of Bruun is valuable for its discussion of the supraspecific implications of karyology in *Primula*. From his analyses, and those of Vogelmann (1960), Valentine (1962), and Kress (1969), it is clear that the genus has several chromosome base numbers (8, 9, 10, 11) that correspond with sectional lines. A base number of $x = 11$ is the most common, and for this reason Bruun believed that it was the primitive condition. This criterion is not necessarily convincing. Wendelbo (1961b) has argued that section *Spondylia*, with a base number of $x = 9$, is the most primitive section of the genus. His evidence lies in the association of

colporoidate pollen, superimposed umbels, folicaceous bracts, and involute vernation. If he is correct, then the $x = 9$ number of this section may be a primitive character shared with section *Aleuritia*. Other sections of the genus with involute vernation have a base number of $x = 11$, and in the genera most closely related to *Primula*, base numbers of 9 (*Androsace*), 10 (*Androsace, Dionysia, Vitaliana*), 12 (*Omphalogramma*), and 19 (*Douglasia*) can be found. At present, the base number of the genus must remain unknown.

Beyond a determination of the somatic or gametic number, extensive karyotyping of *Primula* has not been possible. Chromosomes of diploids tend to be somewhat larger than those of related polyploids (Vogelmann 1960) but all the species seen have relatively small uniform chromomsomes for which little or no morphology can be determined.

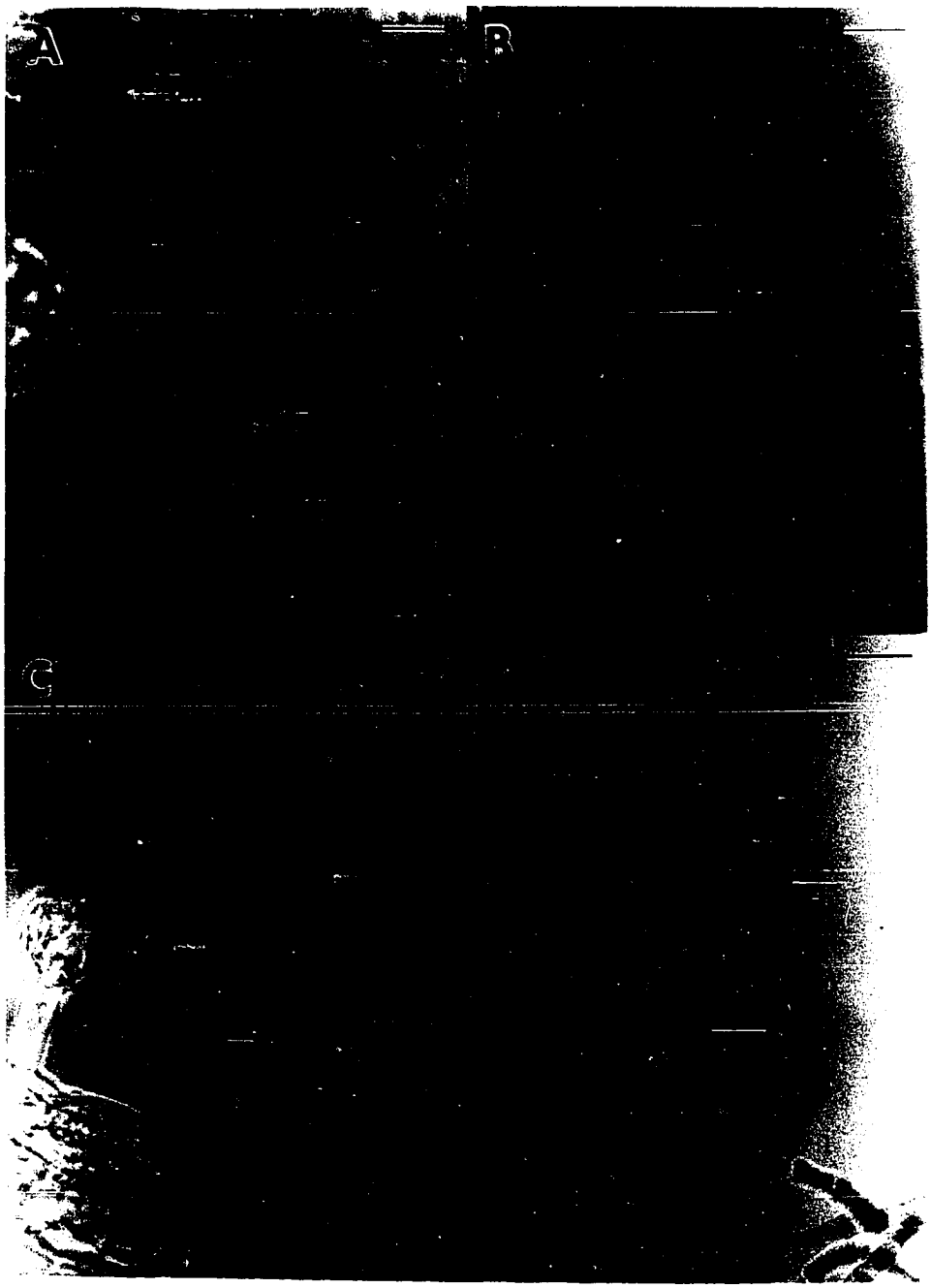
In the sections treated here, polyploidy plays a role only in section *Aleuritia* (x = 9). In sections *Crystallophlomis, Cuneifolia,* and *Armerina* (x = 11) all the taxa are diploid, with the exception of the tetraploid *P. egaliksensis*. While literature reports give the impression that some members of section *Aleuritia* have several chromosome races, in almost all cases it can be shown this is the result of faulty determinations of the voucher specimens rather than inherent cytological variability.

Chromosome number is thus a very strong taxonomic character in *Primula,* both on an intersectional and interspecific basis. While it is not practical for field taxonomy, and even laboratory determinations can be difficult unless appropriate material and sufficient time are available, ploidy level can often be inferred from anatomical features. For example, pollen diameter is a reliable indicator of chromosome number in section *Aleuritia* (see discussion below), and it is likely that it would be equally useful in other groups where polyploidy occurs.

II.Anatomical characters.

Gland size and shape. All species of *Primula* have either articulated hairs or glands on at least some of their vegetative parts. The glands are probably at least relictually farinipotent (section III below), although some glandular species do not produce noticeable farina. Blasdale (1948) was the first to notice that species in different sections of the genus had different shapes and sizes of glands, although until now gland morphology has not been used as a taxonomic character. Figure 1.1

Fig. 1.1. Farinipotent glands in northern species of *Primula*. Scale bar represents 25 μm.
A. Sect. *Aleuritia*: *P. laurentiana*. *Barabe and Chabot on 17 Jun 1940* (DAO).
B. Sect. *Crystallophlomis*: *P. tschuktschorum*. *Kelso 83-103* (ALA).
C. Sect. *Cuneifolia*: *P. cuneifolia* ssp. *saxifragifolia*. *Siplivinsky 806* (ALA).
D. Sect. *Armerina*: *P. nutans*. *Kelso 84-105* (ALA).



shows typical glands and hairs of representatives of the four sections of *Primula* treated here. Sections *Aleuritia, Chrystallophlomis,* and *Cuneifolia* have a large apical cell with one to three smaller basal cells, while section *Armerina* has articulated hairs. Among the glandular sections, the species in section *Cuneifolia* are always efarinose, and a few species within the other two sections may lack farina as well.

Placement and number of glands may be of some taxonomic use at the sectional level. Of the North American sections, only section *Cuneifolia* has glands on the outside of the corolla tube and upper portion of the scape as well as on the vegetative parts. In the other sections, glands are limited to the calyx, the bracts, and the leaf surfaces. Not surprisingly, farinose species have more numerous glands than efarinose ones. Glandular development is particularly noticeable in the heavily farinose *P. eximia* (section *Crystallophlomis),* and in *P. specuicola, P. incana,* and *P. laurentiana* (all in section *Aleuritia*).

Pollen. At the generic level, considerable attention has been given to the usefulness of pollen morphology as a taxonomic and phylogenetic marker in the Primulaceae (Wendelbo 1961c; Punt et al. 1974; Nowicke and Skvarla 1977). Exine ornamentation as well as placement, type, and number of apertures have been used as diagnostic features at the sectional level (Spanowsky 1962). Little attention has been given to a comparative study of pollen morphology at the species level, or to the effects of polyploidy on pollen size and morphology.

My study of pollen morphology of the North American Primulas confirms that exine ornamentation can be a diagnostic sectional character. Pollen of *P. nutans* in section *Armerina* (Fig. 1.2L) has a broadly reticulate exine; in contrast, pollen of taxa in sections *Aleuritia, Crystallophlomis,* and *Cuneifolia* (Fig. 1.2A -J) have a microreticulate exine.

Pollen size is affected by sectional affinity, by ploidy level, and, in distylous species, whether it is produced by a pin or thrum morph. Table 1.1 shows mean pollen sizes for some of the taxa considered here. *Primula cuneifolia* (section *Cuneifolia*) has the largest pollen, followed respectively by species in sections *Crystallophlomis, Armerina,* and *Aleuritia.*

Within section *Aleuritia,* there is a relationship between pollen size and polyploidy (Fig. 1.3). This is a strong correlation up to the hexaploid level, but

Fig. 1.2. Scanning electron micrographs of representative pollen grains in the genus *Primula*. Scale bar represents 10 µm.

A. *P. eximia. Kelso 83-288* (ALA).

B. *P. alcalina. Henderson 4221* (ID).

C. *P. anvilensis. Kelso 84-267* (ALA).

D. *P. cuneifolia* ssp. *saxifragifolia. Kelso 85-20* (ALA).

E. *P. borealis. Kelso 83-292* (ALA).

F. *P. incana. Cooper in 1984* (ALA).

G. *P. laurentiana. Savile and Vaillancourt 1923* (DAO).

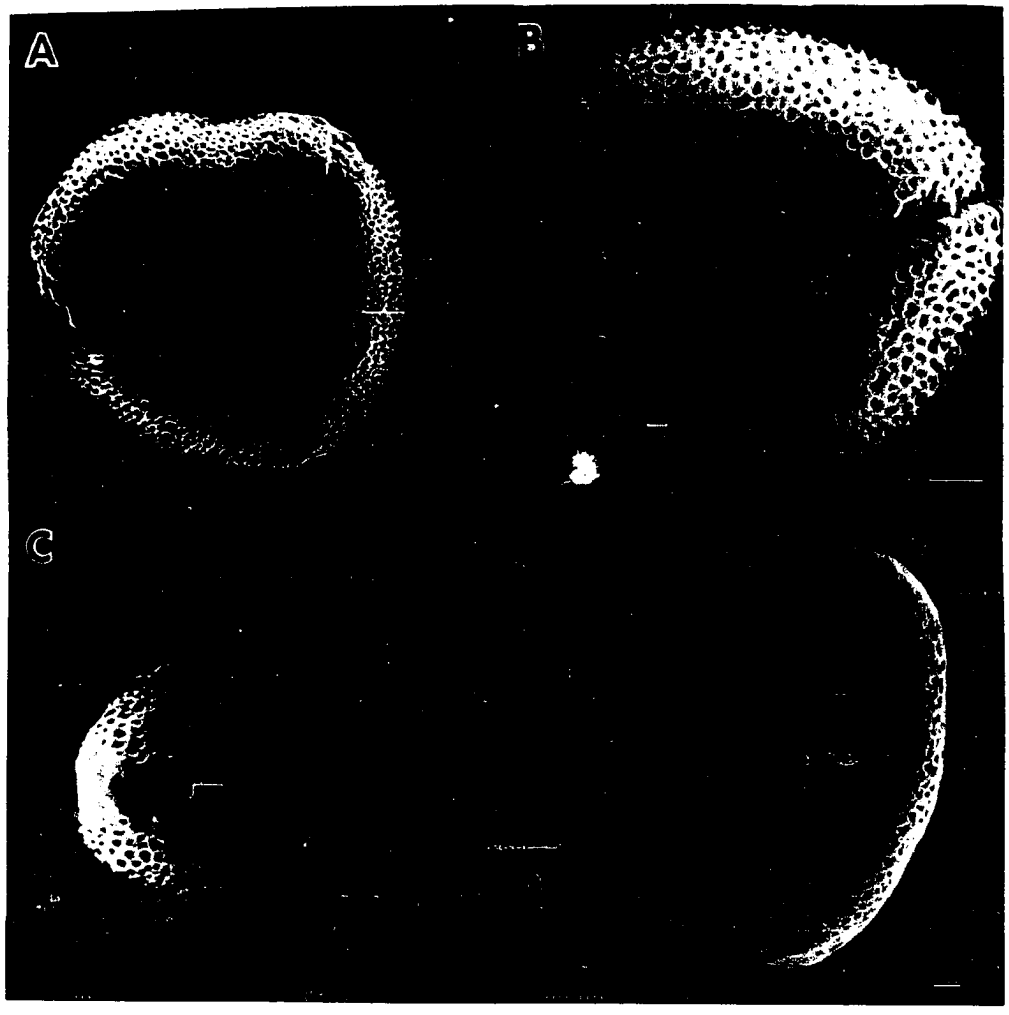
H. *P. scandinavica. Hoeg on 14 Jun 1927* (ALA).

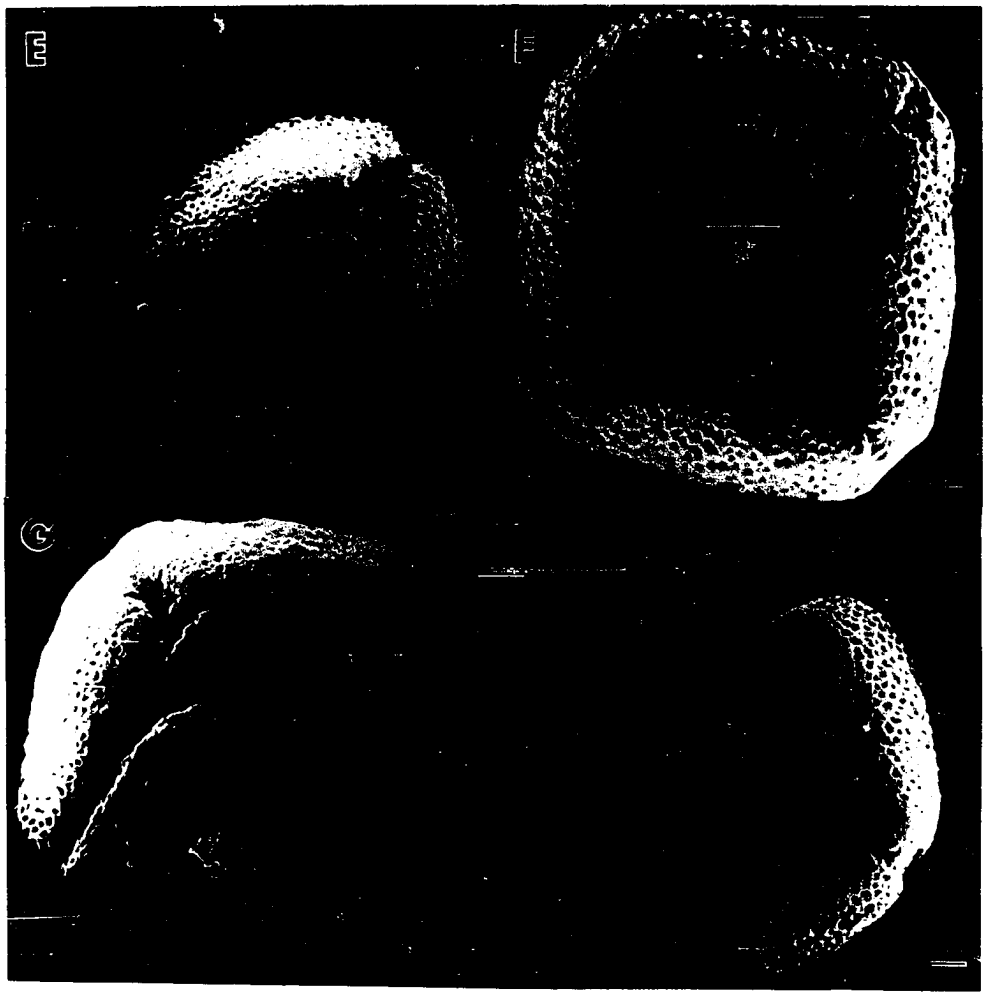
I. *P. scotica. Kelso in Jul 1985* (ALA).

J. *P. stricta. Manning on 21 Aug 1971* (DAO).

K. *P. egaliksensis. Parker 981* (ALA).

L. *P. nutans. Kelso and Holmes 84-21* (ALA).





there are no significant differences in pollen size between the hexaploid, octoploid, and decatetraploid species.

Table 1.1. Pollen sizes of northern Primulas (in microns).

	MEAN DIAMETER (SD)
Sect. *Aleuritia*	
1. *anvilensis* (pin)	11.05 (0.87)
2.*anvilensis* (thrum)	13.97 (1.17)
3. *mistassinica* (pin)	10.79 (0.70)
4. *mistassinica* (thrum)	15.66 (1.10)
5. *borealis* (pin)	13.42 (0.68)
6. *borealis* (thrum)	17.78 (0.80)
7. *incana*	19.20 (1.34)
8. *laurentiana*	19.01 (1.85)
9. *stricta*	19.43 (1.76)
Sect. *Armerina*	
10. *nutans* (pin)	15.77 (0.94)
11. *nutans* (thrum	21.93 (1.18)
12. *egaliksensis*	19.28 (0.88)
Sect. *Crystallophlomis*	
13. *tschuktschorum* (pin)	17.14 (1.06)
14. *tschuktschorum* (thrum)	23.66 (1.46)
15. *eximia*	21.46 (1.97)
Sect. *Cuneifolia*	
16. *cuneifolia / saxifragifolia*	24.83 (1.90)

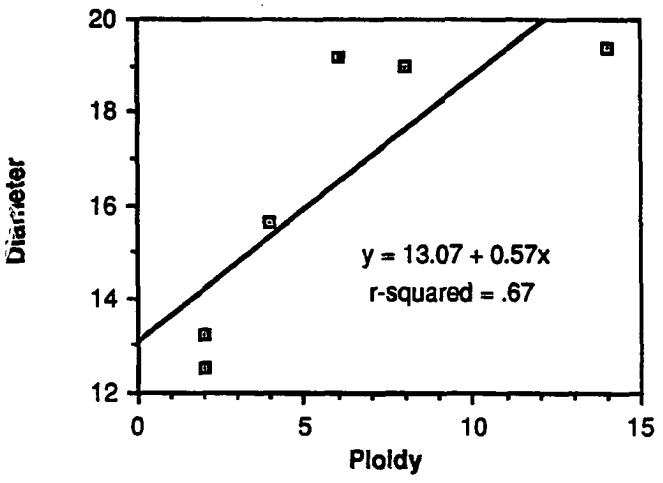


Fig. 1.3. Pollen size and ploidy level in northern species of *Primula*. Filled squares represent the overall mean of pin and thrum morphs in distylous species.

Concommitant with the change in pollen size that occurs with polyploidy, there is a related change in number and placement of colpi. As a taxonomic marker (provided SEM facilities are available), this may be more useful than pollen diameter measurements for the higher levels of polyploidy. Diploid pollen in sections *Aleuritia, Crystallophlomis,* and *Cuneifolia* all have 3-syncolpate pollen (Fig. 1.2B-D). This type is also found in the tetraploid species *P. borealis* of section *Aleuritia* (Fig. 1.2E). Pollen of the hexaploid species *P. incana* (North America) and *P. scotica* (Scotland) show four colpi equally arranged around the equator of the grain (Fig. 1.2F, I). This is identical to the pollen of the octoploid species *P. laurentiana* (North America; Fig. 1.2G) and *P. scandinavica* (northern Europe; Fig. 1.2H). In contrast, the decatetraploid species *P. stricta* (Fig. 1.2J) has 5 fused colpi.

The tetraploid species *P. egaliksensis* (section *Armerina*) is an unusual case. Unlike its close relative, *P. nutans,* which has stephanocolpate pollen (Fig. 1.2L), the pollen of *P. egaliksensis* is 4-syncolpate (Fig. 1.2K). There are additional differences in the exine sculpturing of the the two species. These fundamental palynological characters combined with cytological, anatomical, and morphological ones, are strong evidence of a hybrid background for *P. egaliksensis* (Chapter 5).

The changes in number and arrangement of the colpi as pollen size increases with polyploidy may be due to the harmomegathic functions of the pollen grain, that is, volume changes in response to humidity (Wodehouse 1935; Walker 1976). While much remains unknown about the origin and functions of the exine, it is believed that apertures act both as exit points for the pollen tube, and as regulatory devices controlling water uptake. When pollen size increases as a result of polyploidy, the physical properties of the unit may undergo a reciprocal change that requires a different structural arrangement for proper hydration. While the change in pollen morphology corresponds to a switch from distyly to homostyly in *Primula egaliksensis* and in all the species of section *Aleuritia,* this trend is not repeated in other sections of the genus. *Primula eximia,* the homostylous derivative of *Primula tschuktschorum* (section *Crystallophlomis),* and *P. cuneifolia* subsp. *saxifragifolia,* the homostylous derivative of *P. cuneifolia* subsp. *cuneifolia* (section *Cuneifolia*) show no change in sculpturing or apertural arrangement with a breakdown in distyly. Apertural rearrangements, therefore, most likely represent a mechanical rather than reproductive function.

III. Chemical Characters.

The phytochemistry of the Primulaceae has been studied by Blasdale (1945, 1947); Harborne (1968, 1971); Wollenweber (1974); and Sellmair et al (1977). The nature of the powdery exudate known as "farina" has been of primary interest. Farina is composed of derivatives of the shikimic acid pathway called flavones ($C_{15}H_{10}O_2$). Most farina is white, but some species (e.g. *P. mistassinica* var. *intercedens* of the Great Lakes region, *P. modesta* var. *matsumurae* of the North Pacific, and *P. xanthobasis* of Siberia) have bright yellow farina. Blasdale (1945, 1947) attributes the yellow farina of *P. denticulata* to the presence of the compound

dihydroxyflavone ($C_{15}H_{10}O_4$). Herbarium specimens of some farinose species (e.g., *P. incana*) exhibit both white and cream-colored farina. This could represent the effects of the drying process as well as different chemistry, but it is quite possible that those taxa with yellow farina have some fundamental chemical differences from those with white farina. The differences, however, may not follow taxonomic lines.

It is not clear whether the chemical composition of farina can be of any systematic importance. There is evidence (Harborne 1968) that overall chemical profiles including both leaf and flower pigments can be significant at the generic and sectional levels in the Primulaceae, but at the specific level very little analysis has been done. Basic questions remain about whether farina composition remains constant throughout a species, throughout a population, or throughout the growing season. The common occurrence of efarinose individuals or populations in normally farinose species indicates it is unwise to place too much emphasis on this character.

The function of farina has never been determined. Early explanations for it as an incidental metabolic byproduct are not adequate. The time and location of the secretion of farina strongly suggest it may be an antiherbivory compound like many other flavonoids (Harborne 1982). Stems of young plants, leaf undersides, and inner calyx surfaces surrounding ovules and ripening seeds are uniformly the production sites. If the function of farina is to discourage herbivory, it appears to be successful for I have seen very little evidence of herbivory by insects or microtines on *Primula* leaves.

Detailed studies on the nature of farina in *Primula* need to be undertaken from a systematic and ecological perspective. At the present time, its presence or absence can be used as a taxonomic character at the species level in conjunction with other attributes, but with the dual caveats that all farinose taxa can have efarinose populations or individuals, and that all farinose taxa tend to cease farina production when in fruit.

IV. Ecological Characters.

My investigations indicate that all the North American species of *Primula* show a preference for cool, moist and open habitats, often with disturbance from frost action, flooding, or downslope movement. In addition, there may be further

ecological restrictions. For example, members of section *Aleuritia* show a strong affinity for soils derived from carbonate bedrock. Within this section, *P. borealis* is confined to salt marshes, and *P. incana* to clay soils inland. Other members, particularly the widespread *P. mistassinica,* have less specific habitat requirements. They can be found on cliff faces, lake shores, stream beds, roadsides or around hot springs. In contrast, members of section *Crystallophlomis* show a preference for acid soils, and most are commonly found in frost-disturbed areas. In section *Armerina, P. nutans* on the west coast of Alaska is restricted to salt marshes, but in the interior of the state and in the Yukon, it is found in freshwater marshes where it tolerates saturated soil for much of the growing season. Both subspecies of *Primula cuneifolia* (section *Cuneifolia*) can be found in meadows with a relatively high vegetation cover in comparison to other species of *Primula* ; however, subspecies *saxifragifolia* is most abundant on alpine ridges in open gravel soil with acidic bedrock.

V. Reproductive Characters: Distyly and Homostyly

Primula has long been famous as an example of distyly. We know now the genetic basis of this condition, and that at least in *Primula,* mutations may occur that create homostylous flowers. The frequency of homostyly in *Primula* has been only superficially examined and its taxonomic implications have never been addressed. The reproductive, taxonomic, and biogeographic implications of distyly and homostyly in North American species of *Primula* are discussed at length in Chapter 4. In all the taxa examined here, the condition of distyly or homostyly is one of the most reliable taxonomic markers. In the specimens examined, all individuals of the distylous species were consistently distylous and all individuals of the homostylous species were consistently homostylous. In the genus as a whole, there are only a few examples of homostyle populations in normally distylous species. The most famous of these are the homostyle populations of *P. vulgaris* (Crosby 1940; Curtis and Curtis 1985; Piper et al 1986). *Primula farinosa,* usually distylous and widespread throughout Europe and Asia, is also known for having some homostylous individuals (Smith and Fletcher 1943). This species, which has been given numerous infraspecific names, does need revision, and it is possible that here the homostyles may have some taxonomic significance.

In general, the presence of distyly or homostyly can be regarded as an almost

invariable taxonomic character. Homostyly frequently, but not always, corresponds with polyploidy. All species that have ploidy levels of 6x or higher are homostylous, but diploids and tetraploids usually are distylous. There are examples of closely related distylous and homostylous species at the diploid level. In these cases, the homostylous species is almost certainly derived from the distylous one.

VI. Morphological Characters

A. Leaves. Within the North American species of *Primula,* leaf morphology corresponds closely to sectional lines. The wedge-shaped dentate leaves of *P. cuneifolia* are diagnostic for that section. All species of section *Crystallophlomis* have fleshy lanceolate leaves lacking petioles. As a typical representative of section *Armerina, P. nutans* is strongly petiolate, with thin, oval or elliptical blade. Within section *Aleuritia,* all species have spathulate to oblanceolate leaves. In any section it is not unusual to have several slightly different leaf shapes on a single plant.

Because most *Primula* species bloom soon after snowmelt, their leaves are not fully expanded at anthesis. The leaves enlarge over the growing season, and by the time the capsules are ripe they may be up to four times their length at early anthesis. In addition, vegetative growth in *Primula* is extremely responsive to nutrient availability. Luxuriant forms in all species can be seen in nutrient rich areas, such as sites with resident bird populations or around human habitations.

With the exception of *Primula cuneifolia* s. lat. which has consistently dentate leaves, the nature of the leaf margins can be highly variable. *Primula eximia* usually has entire leaves, but they may also be serrate to widely denatate. *Primula nutans* has consistently entire leaves, but the leaves of its relative *P. egaliksensis* may have entire, or in age, widely denticulate margins. Within section *Aleuritia,* leaf margins may be a reliable taxonomic character at the species level (e.g. *P. specuicola, P. anvilensis*), or they may be entirely variable (e.g. *P. incana, P. stricta*).

B. Bracts. All species of *Primula* have 3-6 involucral bracts subtending the umbel of flowers. Certain attributes of these bracts may be used as taxonomic characters at the sectional and specific level. In the sections examined here, these include overall shape at the tip (involute or flat), shape at the base (plane or saccate), and the presence or absence of auricles.

C. Height. There are distinct differences in height between species of *Primula*. Scape height is most reliable as a taxonomic character when measured at full (the point at which most of the flowers in the umbel are blooming) or late anthesis. Several of the arctic species begin blooming very early when plants are almost ascapose. Elongation of the scape continues throughout anthesis until the capsules are ripe. Thus, the fruiting plant can be several times as tall as the plant in first bloom. This increase is particularly dramatic in some of the taller species such as *P. incana* and *P. laurentiana*.. These two taxa are frequently misidentified as their shorter relatives, *P. stricta* and *P. mistassinica* respectively, when collected in the early stages of flowering with short scapes. Figure 1.4 demonstrates the degree to which this elongation of the scape occurs in *P. incana*.

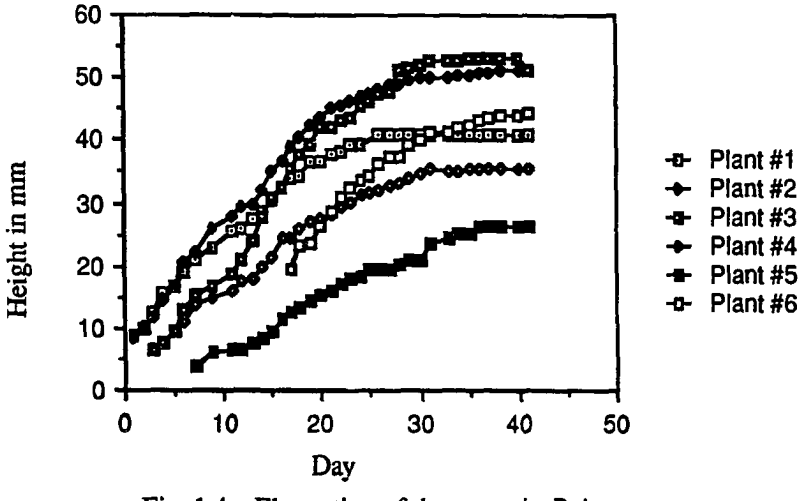


Fig. 1.4. Elongation of the scape in *P. incana*.
Day 1 = first flower in umbel opens

D. Pedicels. As capsules ripen and elongation of the scape slows and eventually ceases, elongation and stiffening of the pedicels begins. At anthesis, the length and the habit (capillary or erect) of pedicels are both strong taxonomic characters at the species level. In fruit, however, much elongation and stiffening occurs and the fruiting umbel looks very different from the blooming umbel. Presumably these changes relate to seed dispersal. Seeds are shaken out of the capsules by wind or passing animals, and erect elongated pedicels may increase dispersal distance from the parent plant. The process of elongation begins as scape elongation ceases, and is very rapid (Figure 1.5).

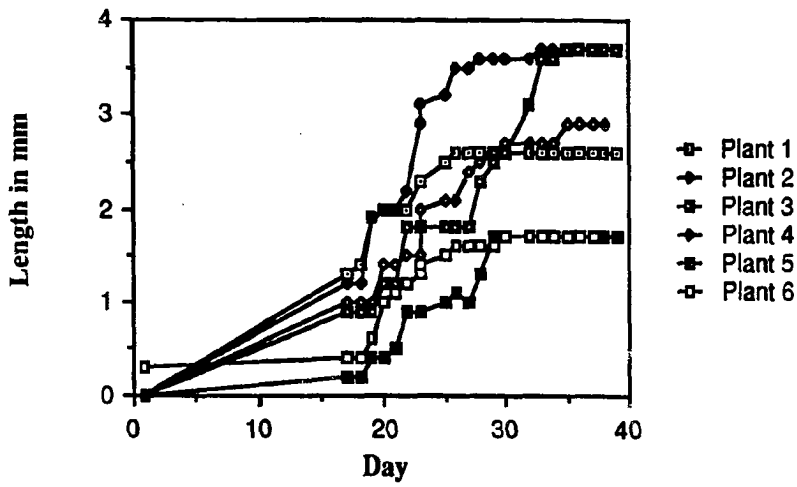


Fig. 1.5. Elongation of the pedicel in *P. incana*.
Day 1 = first flower in umbel opens.

E. Flower number. The number of flowers per umbel of any individual plant appears to be a a function of several factors, including nutrients and available growing season. Plants growing in highly fertilized sites tend to have more flowers per umbel than individuals of the same taxon growing in nutrient-poor sites. In species with multi-flowered umbels, flowering is asynchronous. Those individuals that emerge early from snow cover have a longer growing season in which they can

develop flowers than those plants that emerge later. *Primula eximia,* for example, exhibits few flowered umbels when growing in late snow beds, and many flowered umbels in sites with early snow melt.

While ecological factors undoubtedly play some role in influencing flower number in any individual plant, species-specific reproductive factors are clearly also involved. Higher flower numbers are correlated to some extent with homostyly in section *Aleuritia*. This may be due to the effects of polyploidy as well as the autogamy that is a product of homostyly (Chapter 4).

F. Calyx morphology. Calyx size in any species of *Primula* is generally correlated with overall size of the individual plant. Individuals with small corollas have small calyces. There are, however, strong sectional differences in other aspects of calyx morphology, particularly shape, color, and the degree to which the calyx tube is divided. In all the sections examined here (but not in all sections of the genus as a whole), the calyx is divided by lanceolate teeth. In section *Crystallophlomis* it is campanulate, ribless, green to greenish-black, and deeply divided almost to the base by narrow teeth. In section *Armerina* the calyx is cylindrical, ribless, green or green with purple striations, and divided less than 1/4 its length. In section *Cuneifolia* the calyx is broadly urceolate, ribless, green, and divided to 1/2 or more. Species in section *Aleuritia* generally have a campanulate, obscurely ribbed, green or green and purple calyx that is divided 1/3 to 1/2 by lanceolate teeth.

While overall calyx morphology can be a useful character to distinguish between sections, it is less useful at the species level. At least in section *Aleuritia* in North America with a closely related diploid-polyploid complex where at least some of the members are highly inbred, calyx structure is not a reliable taxonomic character to distinguish species.

G. Corolla morphology. Several aspects of corolla morphology are useful as taxonomic markers. These include the tube, the limb, the lobes, and color.

The length of the corolla tube relative to the calyx can be diagnostic at the species level. This is consistent during the period of anthesis; however, in all taxa the tube elongates rapidly between bud stage and when the flowers open. Therefore, positions can be measured accurately only when plants are in full bloom.

Within a certain range, width of the corolla limb is another diagnostic character. In all sections there is some infraspecific variation that is probably related to ecological factors. In general, corolla size in taxa with small flowers varies less than in taxa with larger flowers, and on the whole, distylous taxa have larger flowers than homostylous ones.

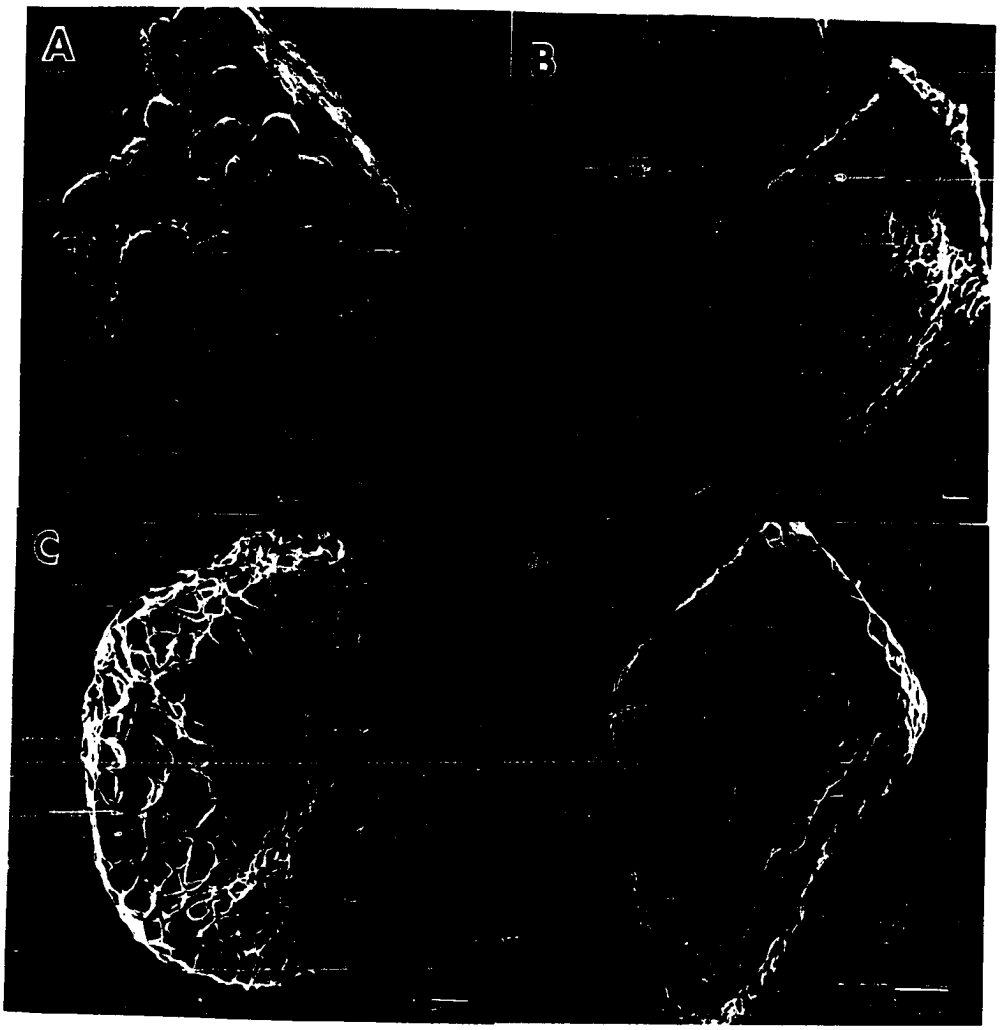
With the exception of section *Crystallophlomis*, all the taxa studied here have emarginate corolla lobes. In small-flowered taxa (e.g. *P. egaliksensis, P. incana*) the division of the lobes is consistently shallow. In the larger flowered taxa (eg. *P. borealis, P. cuneifolia*) the division of the lobes tends to be deep, but it can be variable even within a single population.

Albino flowers can be found in any species of *Primula*.. Beyond these exceptional specimens, however, flower color can be a very useful taxonomic character at both the sectional and species level. Species in section *Crystallophlomis* have magenta flowers, those in section *Cuneifolia* have rose-pink flowers, and those in sections *Aleuritia* and *Armorina* have violet or white flowers. Flower color is deepest in buds and young flowers and gradually fades as the flower matures. This is particularly noticeable in the violet-flowered species in section *Aleuritia.* where older flowers on herbarium specimens can look almost white. With the exceptions of *P. egaliksensis* which appears to have equally abundant white and lavender morphs throughout its range, and *P. mistassinica* which has a white morph Newfoundland, all the taxa studied here are consistent in their flower color.

H. Capsule Morphology. Capsule morphology follows sectional lines. Taxa in section *Cuneifolia* have globose capsules, those in section *Crystallophlomis* have broadly cylindrical capsules, those in section *Aleuritia* have elliptical to cylindrical capsules, and those in section *Armorina* have narrowly cylindrical capsules. Capsules of the related species in section *Aleuritia* are difficult to distinguish except on the basis of size. Length of the capsule relative to the length of the calyx is the most relevant size component for taxonomic purposes in all sections.

I. Seed Morphology. Except at the sectional level, seed morphology in *Primula* is too uniform to be of taxonomic value. Seeds of section *Crystallophlomis* (Fig. 1.5a) have noticeably vesiculate coats and are relatively large (greater than 1 mm in

Fig. 1.6. Seed coat morphology in the genus *Primula*. Scale bar represents 50 µm.
A. Sect. *Crystallophlomis: P. eximia*. *Kelso 82-288* (ALA).
B. Sect. *Cuneifolia: P. cuneifolia* ssp. *cuneifolia*. *Friedman 3* (ALA).
C. Sect. *Aleuritia: P. borealis*. *Kelso 83-292* (ALA).
D. Sect. *Armerina: P. nutans*. *Kelso and Holmes 84-21* (ALA).



diameter) while those of sections *Cuneifolia, Armerina,* and *Aleurita* (Fig. 1.5b-d, respectively) have reticulate coats and are quite small (less than 0.5 mm in diameter). Seeds of *Primula cuneifolia* s. lat. are unique in having flanged edges. Within the large section *Aleuritia*, seed coats are too similar to distinguish between species. While there may be some differences in seed size due to levels of polyploidy, they are too slight to be useful as a taxonomic character.

Table 1.2 summarizes the taxonomically useful characters in *Primula.*

Table 1.2. Summary of taxonomically useful characters in *Primula.* Asterisk indicates that the character may differ at the species level or below.

	Aleuritia	*Armerina*	*Crystallophlomis*	*Cuneifolia*
BASE NUMBER	9	11	11	11
PLOIDY LEVEL	2x-14x *	2x-4x *	2x	2x
GLAND TYPE	capitate	jointed hairs	capitate	capitate
GL. LOCATION	ca, br, lvs	ca, br	ca,br,lvs	ca,br,lvs,cor,scape
POLLEN DIAMETER	10-20 µm *	15-23 µm *	17-25 µm	20-25 µm
EXINE	microreticulate	reticulate	microreticulate	microreticulate
NO. OF COLPI	3-5 *	4-6 *	3	3
FARINA	yes or no *	no	yes or no *	no
HABITAT	calcareous	wet	acidic	acidic
BREEDING SYSTEM	distyly, homostyly *	distyly, homostyly *	distyly, homostyly *	distyly homostyly *
LEAF SHAPE	spathulate	ovate-elliptical	lanceolate	cuneate
LEAF MARGINS	denticulate	entire	variable	coarsely dentate
BASE OF BRACTS	plane or saccate	saccate and auriculate *	plane	plane
SCAPE HEIGHT	variable *	variable	variable	variable
PEDICELS	capillary or upright *	capillary	capillary	capillary
FLOWER NO.	variable *	2-5	2-many	1-4
CALYX SHAPE	campanulate	cylindrical	campanulate	urceolate
CALYX RIBS	obscure	absent, obscure *	obscure	obscure
CALYX COLOR	green, purple	green, purple	green, black	green
DIVISION BY TEETH	1/3-1/2	<1/4	3/4+	1/2+
COROLLA TUBE	equal, exserted	exserted	exserted *	exserted
LIMB WIDTH	5-15 mm *	5-15 *	15-25	15-25
FLOWER COLOR	white or lilac *	white or lilac	magenta	rose-pink
CAPSULE SHAPE	elliptical	narrowly cylindrical	broadly cylindrical	urceolate
SEED COAT	reticulate	reticulate	vesiculate	reticulate, flanged

Chapter Two

Taxonomy of the genus *Primula* in North America: sections *Aleuritia, Armerina, Crystallophlomis,* and *Cuneifolia.*

PRIMULA L.

Herbaceous perennial or rarely annual herbs. Leaves flattened or tufted rosettes, persistent or deciduous; petiolate or sessile; blade simple or lobed; margins entire or dentate. Flowers usually showy, in scapose umbels, capitula, racemes or rarely solitary, subtended by a whorl of 3-6 lanceolate involucral bracts. Calyx 5-parted, persistent, tubular, campanulate, or diskoid. Corolla funnelform, salverform, or campanulate, deeply lobed; tube elongate; lobes patent or erect, entire or emarginate. Stamens 5, epipetalous; anthers introrse. Flowers often distylous, sometimes homostylous. Stigma globose, capitate, or somewhat lobed; ovary superior, globose, with free central placentation. Fruit a globose, ovate, elliptical, or cylindral capsule, opening by short teeth, valves, or irregular disintegration of the capsule wall. Seeds many, ovoid-angular to subglobose, dorsally flattened.

Key to the sections and species of *Primula* in North America (exclusive of section *Parryi* of western North America)

1. Flowers lavender or white; limb 12 mm in diameter or less; leaves thin, not at all fleshy.
   2. Leaf blades ovate or elliptical, distinctly petiolate; plants completely efarinose (section *Armerina*)
      3. Involucral bracts distinctly auriculate at the base; flowers 8 mm or more in diameter.....*P. nutans*
      3. Involucral bracts saccate at base but not auriculate; flowers less than 8 mm diameter.....*P. egaliksensis*
   2. Leaf blades spathulate or lanceolate, not distinctly petiolate; plants generally somewhat farinose (section *Aleuritia).*
      4. Flowers distylous.
         5. Involucral bracts saccate or gibbous at base; plants of coastal salt marshes.....*P. borealis*

5. Involucral bracts plane at base; plants not of coastal salt marshes.....6
   6. Corolla limb always white.
      7. Plants farinose; pedicels erect at anthesis, shorter than bracts; plants of Idaho.....*P. alcalina*
      7. Plants efarinose; pedicels capillary at anthesis, longer than bracts; plantsof the Seward Peninsula, Alaska.....*P. anvilensis*
   6. Corolla limb lavender, rarely white.
      8. Leaves heavily white farinose; plants of cliff faces in southern Utah and Arizona.....*P. specuicola*
      8. Leaves efarinose or bright yellow farinose; plants of boreal regions.....*P. mistassinica*
4. Plants homostylous.
   9. Corolla limb 8 mm or more in diameter.....*P. laurentiana*
   9. Corolla limb less than 8 mm diameter.....10
      10. Leaves and calyces slightly farinose; capsules ovate, only slightly longer than calyx; plants of estuarine habitats east of the Mackenzie River .....*P. stricta*
      10. Leaves and calyces heavily farinose; capsules cylindrical and strongly exserted from calyx; plants not of estuarine habitats or found east of Hudson Bay.....*P. incana*

1. Flowers deep pink to magenta; limb greater than 12 mm diameter, leaves somewhat fleshy.
   11. Leaf blades cuneate, margins strongly dentate; flowers deep pink, lobes distinctly emarginate (section *Cuneifolia).*
      12. Flowers distylous.....*P. cuneifolia* subsp.*cuneifolia*
      12. Flowers homostylous.....*P. cuneifolia* subsp. *saxifragifolia*
   11. Leaf blades lanceolate, margins entire to widely denticulate; flowers magenta, lobes entire or slightly emarginate (section *Crystallophlomis)*
      13. Flowers distylous.....*P. tschuktschorum*
      13. Flowers homostylous.....*P. eximia*

Primula section **Aleuritia** (Duby) Wendelbo, Arbok Univ. Bergen, Mat.-Naturvitensk. Ser. 1961: 37. 1961. TYPE SPECIES: *P. farinosa* L. Plants usually farinose or with farinipotent glands, lacking rhizomes. Leaves with revolute vernation, blades decurrent, lanceolate to spathulate, glabrous. Inflorescence a simple umbel subtended by involucral bracts usually saccate or gibbous at base, rarely plane. Flowers lilac, pink, purple, or white; corolla lobes notched or cleft. Chromosome base number: $x = 9$.

Distribution: Cosmopolitan, north temperate latitudes, one southern hemisphere representative. North American representatives:

P. alcalina Cholewa and Henderson (Idaho)

P. anvilensis Kelso (Alaska)

P. borealis Duby (Alaska, Yukon, NE Asia)

P. incana Jones (Alaska-Colorado)

P. laurentiana Fernald (eastern Canada)

P. mistassinica Michx. (boreal)

P. specuicola Rydb. (Utah, Arizona)

P. stricta Hornem. (Canadian Arctic, European Arctic)

Primula alcalina A. Cholewa and D. Henderson (Fig. 2.1)

Primula alcalina A. Cholewa and D. Henderson, Brittonia 36: 59-62. 1984. TYPE: UNITED STATES. IDAHO. Lemhi Co., 10 mi. north of Blue Dome along Birch Creek, *Henderson and Cates 1372* (Holotype: ID; Isotype: NY).

DESCRIPTION

Plants farinose only when young, efarinose in age. Scape 6.5-24 cm high. Leaves elliptic-oblanceolate, blade narrowing gradually onto winged petiole, 1-4 cm long, margins crenulate or denticulate, sometimes entire. Involucral bracts plane at base, 0.4-0.7 cm long, lanceolate, apex obtuse or acute. Umbel 3-10 flowered, pedicels erect, to 0.5 cm long. Flowers distylous. Calyx campanulate, somewhat farinose, obscurely ribbed, 4-6.5 cm long, green or with purple striations, lobed about one third its length, teeth with capitate glands. Corolla white, throat yellow; tube 0.4-0.7 cm long; limb 0.6-1 cm wide, lobes deeply cordate. Stamens ca 1.5 mm long, anthers located towards the middle of the corolla tube. Stigma capitate, in pin plants located in upper third of corolla tube, positions reciprocal in thrum plants. Pollen ca 10 μm diam. in pin plants, ca 12 μm diam. in thrum plants, exine microreticulate, 3-syncolpate. Chromosome number: $n = 9$ (Idaho: Cholewa and Henderson 1984).

Habitat: Wet alkaline meadows; associated species: *Dodecatheon pulchellum* (Raf.) Merr., *Phlox kelseyi* Brittton, *Potentilla fruticosa* L., *Valeriana edulis* Nutt. (Cholewa and Henderson 1984).

Range: Endemic to northeastern Idaho west of the Lemhi Range (Fig. 2.2)

Representative specimens examined.

IDAHO. Clark Co.: ca 3.5 mi N of Lone Pine, *Henderson 4221* (ID). Custer Co.: ca 26 mi NW of Howe along Summit Creek, *Henderson et al 4484* (ID),*Williams 13-50* (NY); Lower Summit Creek, *Anderson and Davies 133* (ID). Lemhi Co.: upper bridge on Birch Creek, T11N R29E, *Davis 3118* (ID); along Birch Creek, *Christ 17 May 1947* (ID); near Reno, T111N R29E S27, *Bond 20232* (ID); 2 mi N

1719 (NY); 20 mi SE of Gilmore along Birch Creek *Hitchcock 23860* (COLO, DAO); 5.4 mi N of Lone Pine, upper Birch Creek *Cholewa 858* (ID).

DISCUSSION

Primula alcalina is most similar to *P. incana* Jones, with which it was initially confused until it was described by Cholewa and Henderson (1984) as a distinct species. *P. alcalinea* is a narrow endemic of northern Idaho, distinguished from *P. incana* by its white, distylous flowers, efarinose leaves, and diploid rather than hexaploid chromosome number.

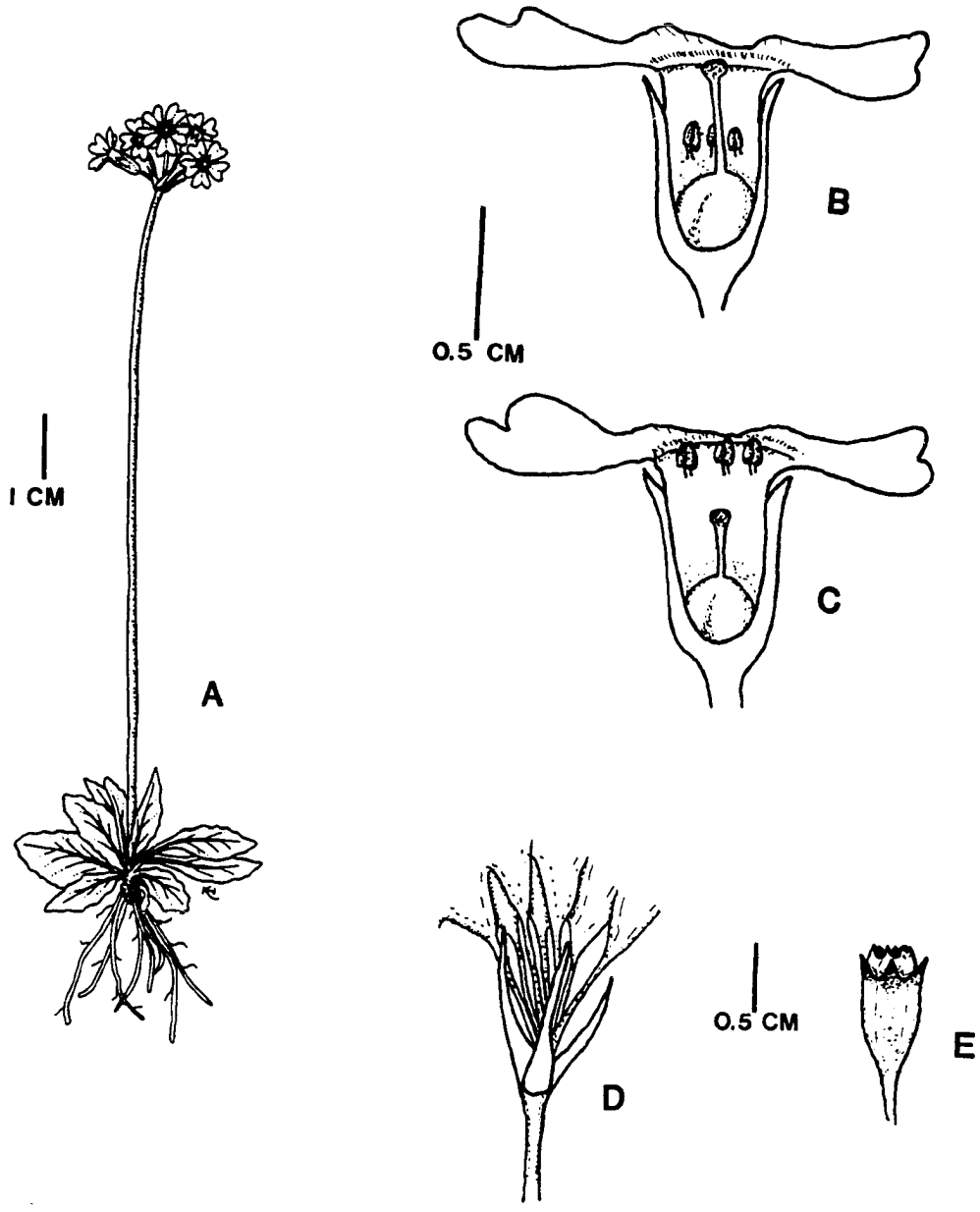


Fig. 2.1. *Primula alcalina.* A. Habit. B. Pin flower. C. Thrum flower. D. Bracts E. Capsule.

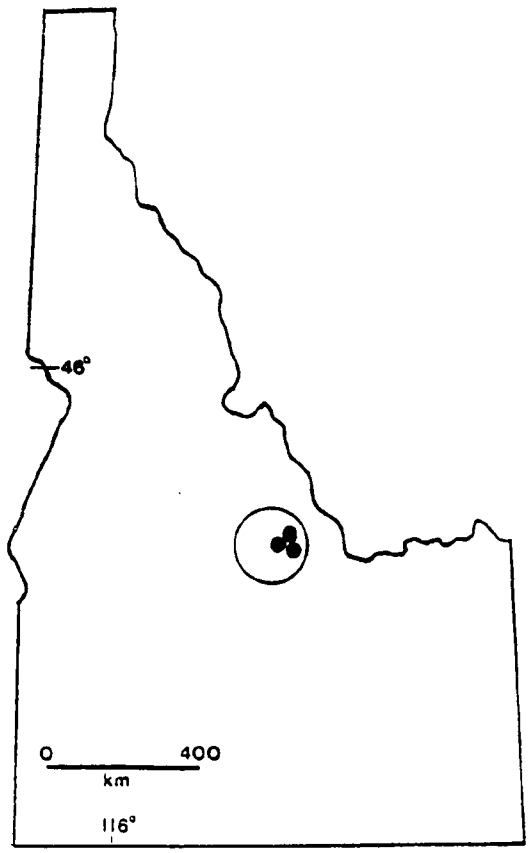


Fig. 2.2. Known range of *Primula alcalina*.

Primula anvilensis S. Kelso (Fig. 2.3)

Primula anvilensis S. Kelso, Systematic Botany 12: 9-13. 1987. TYPE: UNITED STATES. ALASKA. Nome area, Anvil Mt., *Kelso 83-136.* (Holotype: ALA; Isotypes: COLO, NY, CAN)

P. parvifolia Fernald (non Duby), Rhodora 30: 93. 1928., Hultén, Fl. Alaska and Yukon, Acta. Univ. Lund 4: 1273. 1948.

DESCRIPTION

Plants slender, efarinose. Scape 2-10 (12.5) cm tall. Leaves bright green, cuneate or spathulate, including the petioles 0.5-1(2) cm long, margins strongly denticulate near the apex; the blade 0.2-0.4 cm wide, gradually narrowing onto a winged petiole 0.2-0.4 cm long. Involucral bracts lanceolate, 0.2-0.5 cm long, plane at the base. Umbel 1-5 (7) flowered; pedicels filiform, 0.5-1 cm long. Flowers distylous. Calyx efarinose, campanulate, obscurely ribbed, 0.2-0.4 cm long, green or with purple striations, divided to one third its length, teeth lanceolate with capitate glands. Corolla white with a yellow throat; limb 0.5-0.8 cm wide, emarginate; tube equal to the calyx or only slightly longer. Stamens 0.5-0.75 mm long, anthers located in the lower third of the corolla tube in pin plants. Stigma capitate, located in the upper third of the corolla tube in pin plants, positions reciprocal in thrum plants. Pollen dimorphic, ca 11 μm diam. in pin plants and ca 13 μm diam. in thrum plants; exine microreticulate, 3-syncolpate. Capsule cylindrical, 0.3-0.5 cm long, strongly exserted from the calyx; seeds brown, strongly reticulate, 0.5 mm long. Chromosome number: $2n = 18$ (Nome: *Kelso 83-136* at ALA).

Habitat: Frost boils, late snowbeds, creek banks and gravel bars with calcareous substrates; in alpine herb-sedge associations found with *Androsace chamaejasme* Host, *Salix reticulata* L., *Saxifraga nelsoniana* D. Don, *Saxifraga oppositifolia* L., *Silene acaulis* (L.) Jacq.

Range: An endemic species of the Seward Peninsula, northwestern Alaska (Fig. 2.4)

Representative specimens examined.

UNITED STATES. ALASKA. Seward Peninsula, Anvil Mountain: *Heller 963* (ALA), *Kelso 82-41A, 83-183, 83-205, 83-206, 83-60* (ALA), *Miller 316C* (ALA); Banner Creek:*Walker in 1970* (ALA); Bendeleben Mountains: *Kaufman 26 Jun 1984* (ALA); Cape Nome: *Blaisdell in 1900* (NY), *17''* (GH); Casadepaga: *Kaufman 7 Jul 1984* (ALA), *Kelso 84-388* (ALA); Council: *Kelso 83-40* (ALA); Crete Creek: *Kelso 82-70* (ALA); Dexter: *Heller 864* (ALA); Don River: *O'Brien and Lederer in 1983* (ALA); Elim: *Anderson 3356* (ISC); Gold Bottom Creek: *Kelso 84-126* (ALA); Grand Central River: *Kaufman 79* (ALA); Kougarok Road: *Kelso 83-08, 83-87, 83-192* (ALA), *Springer in 1970* (ALA), *Zachel in 1970* (ALA); Lost River: *Lenarz 42, 61* (ALA); Mount Osborn: *Kelso 84-330* (ALA); Mt. Wick: *Kaufman 27 Jun 1984* (ALA); North Newton Peak: *Williams 487* (ALA); Nome: *Anderson 3179* (ISC),*3205* (ISC, K), *3231B* (ISC), *Hanson 169* (ISC), *Hutchinson 243-48* (K), *Kelso 83-100, Kessel 3 July 1966, Miller 316E* (ISC), *Thornton 2137* (K), *Whillans 24* (DAO); Omilak Mountain: *Kaufman 49* (ALA); Rock Creek: *Kelso 84-267* (ALA); Salmon Lake: *Batten 74-36* (ALA), *Kelso 82-127* (ALA), *Welsh 5903* (ISC); Solomon River: *Kelso 83-83* (ALA), *Parker 302* (ALA); Teller: *Kelso 83-218A* (ALA), *Williams 3394* (ALA); Teller Road: *Kelso 83-52, 83-200* (ALA), *Williams 3366* (ALA); Tubutulik: *Kelso 84-390* (ALA); Upper Fox River: *Parker 253* (ALA); Wales: *Kelso 81-181, 82-4, 83-292A* (ALA), *Kelso et al. 181* (ALA, COLO).

DISCUSSION

The species we now know as *Primula anvilensis* was first described as an Alaskan taxon in the early 1900's, when the first plant collections were made in the Nome area. Its identity was lost, however, in an unfortunate nomenclatural confusion with another species of western Alaska, *Primula borealis* Duby. It was not until recently that the taxon was clearly distinguished as a separate species under the name *P. anvilensis* by Kelso (1987a).

Primula borealis is an arctic-maritime species with a center of distribution around the Bering Strait between Alaska and eastern Asia. It is characterized by a large-flowered umbel on short pedicels, violet corollas with a tube well-exserted from the calyx, saccate or gibbous bracts subtending the pedicels, and elliptical leaves that vary in size. The original monograph of Duby provided a brief diagnosis of a second species, *Primula parvifolia*, based on Langsdorff material from the

southern Bering Sea region (distributed as *P. araboides,* nomen nudum, from herb. Fischer E! K! NY!). Duby did not clearly distinguish *P. parvifolia* from *P. borealis* except on the basis of leaf size, and *P. parvifolia* was treated as a synonym of *P. borealis* by other authors of the time.

Fernald (1928), in a revision of section *Aleuritia* (then called section *Farinosae*), noted a collection (Cape Nome, *Blaisdell 129:* GH! NY!) from the Seward Peninsula that was morphologically distinct from *P. borealis.* He identified the specimens as *P. parvifolia* Duby and wrote a detailed description of the species based on characteristics of the Seward Peninsula plants. In sharp contrast to the typical morphology of *P. borealis,* diagnostic features of this taxon included a delicate stature, filiform pedicels, small corollas, and nonsaccate involucral bracts.

The treatment by Fernald as well as the name *P. parvifolia* was accepted by Hultén (1948). The first of any of the twentieth century taxonomists to have experience with the species in question, Hultén noted the clear differences between *P. borealis* and *P. parvifolia* sensu Fernald and maintained them as two species. In his subsequent manual of the flora (1968), however, he combined the two following Smith and Fletcher (1943) who conclusively showed that *P. parvifolia* was a synonym of *P. borealis.* Thus, because of the erroneous use by Fernald of the name *P. parvifolia,* the identity of the Seward Peninsula taxon was lost when that name was subsumed under *P. borealis.*

Specimens of *P. anvilensis* (*Hutchinson 213-218, 313-331,* E! K!) incorrectly identified as *Primula stricta* Hornem. led Hultén (1968) to map this latter species as present in Alaska on the Seward Peninsula. Porsild (1939) also identified several Seward Peninsula specimens of *P. anvilensis* as *P. stricta* (*Porsild 1381, 1382, 1445,* CAN!). *Primula stricta* is found in the Canadian Arctic and in Greenland. It is characterized by a capitate umbel of violet flowers on very short pedicels, a farinose calyx, saccate bracts, and a high chromosome number ($2n = 126$). It is not a close relative of *P. anvilensis* and should be excluded from the Alaskan flora.

Primula anvilensis is very common throughout the Seward Peninsula in Alaska but it has not been found on the Soviet side of the Bering Strait (B. Yurtsev, pers. comm.) nor along the Bering or Chukchi Sea coasts of Alaska. It is one of the plant taxa endemic to the region known as Beringia, along with *Artemisia senjavinensis* Besser, *Artemisia globularia* Besser, *Papaver walpolei* Porsild, and *Saxifraga nudicaulis* D. Don. Unlike these species, however, *P. anvilensis* appears to be wholly North American in distribution.

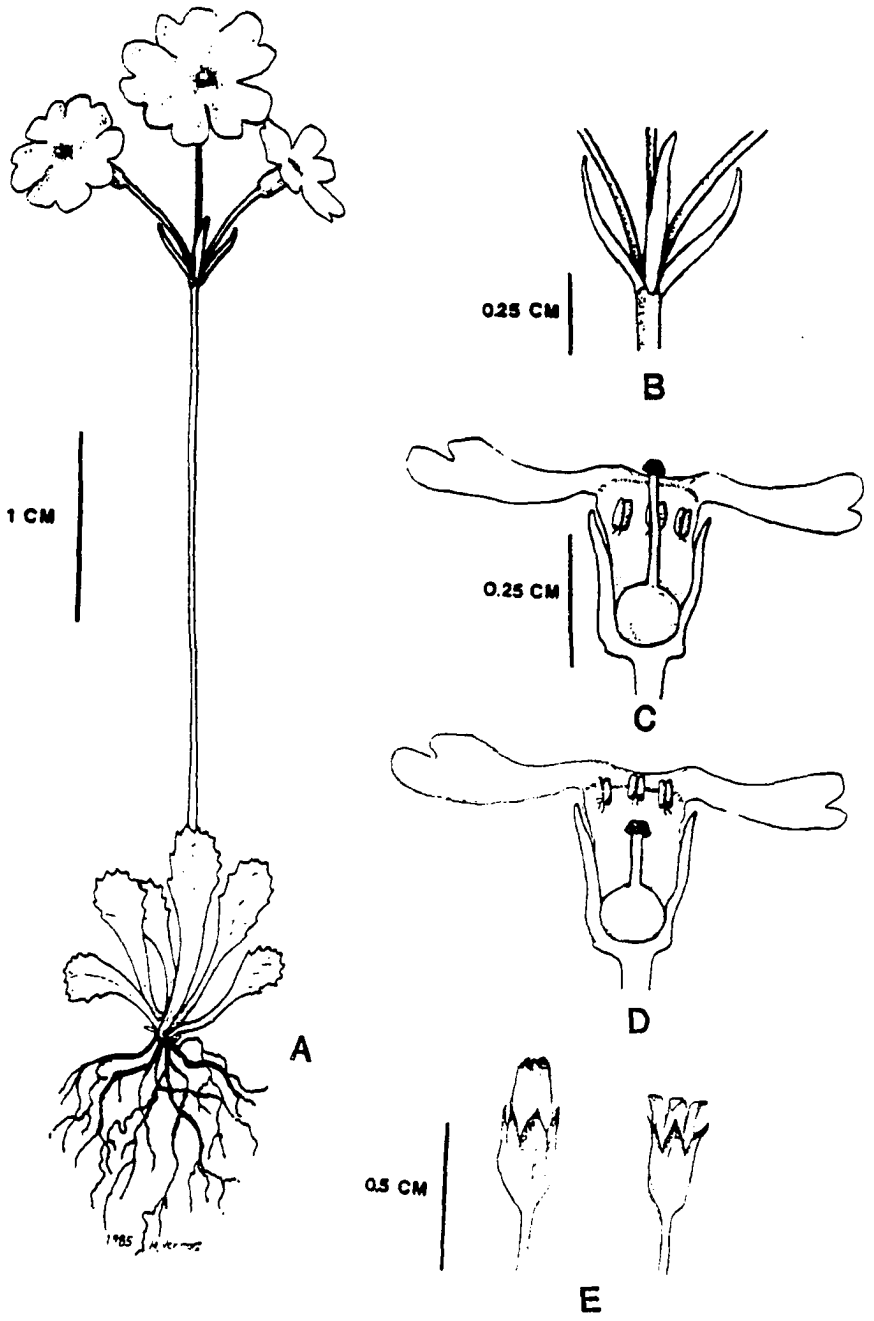


Fig. 2.3. *Primula anvilensis*. A. Habit. B. Bracts. C. Pin flower. D. Thrum flower. E. Capsule.

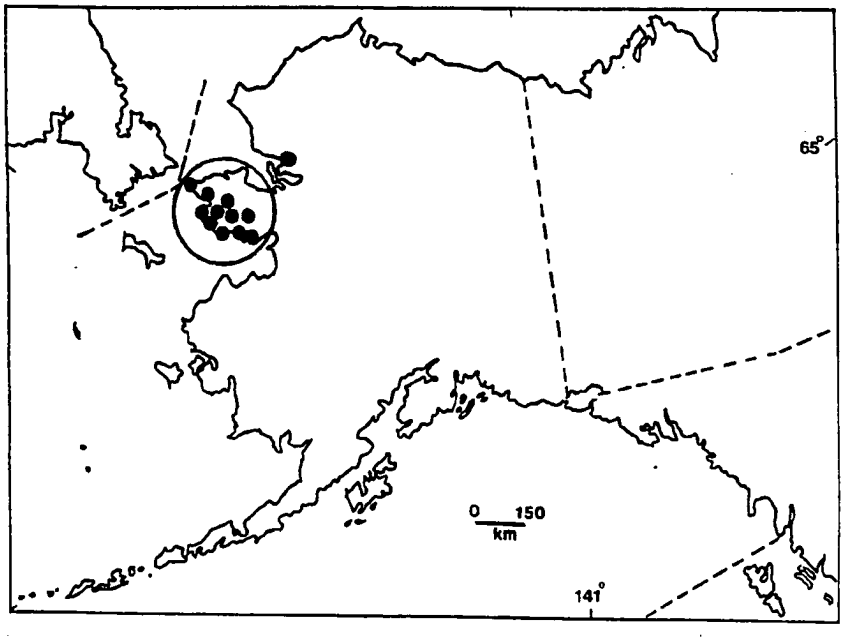


Fig. 2.4. Known range of *Primula anvilensis*.

Primula borealis Duby (Fig. 2.5)

Primula borealis Duby, Mem. Soc. Phys. d'Hist. Nat. Génève 10:31. 1843; in DeCandolle, Prodromus 8:443. 1844. TYPE: UNITED STATES. ALASKA: Shishmaref. *Chamisso and Eschscholtz in 1816.* (Holotype: LE; photograph E!).

Primula mistassinica Chamisso and Schlechtendal (nec Michaux), Linnaea 1: 213-215.1826.

Primula parvifolia Duby, in DeCandolle, Prodromus 8: 42. 1844.

Primula borealis var. *parvifolia* (Duby) Pax, in Engler, *Pflanzenreich,* Primulaceae, 81. 1905. TYPE: "Ad fretum Beering" as *P. araboides*, nomen nudum, herb. Fischer (Holotype: LE? isotypes: E! K! NY!)

Primula tenuis Small, Bull. Torr. Bot. Club 25: 320. 1898. TYPE: UNITED STATES. ALASKA: Pastolic. *Dall 25 Jun 1871.* (Holotype: NY! photograph E!)

Primula chamissonis Busch, *Fl. Sib. & Orient. Extrem.* 4: 28. 1926. TYPE: UNITED STATES. ALASKA. Kotzebue. *Chamisso in 1816-17.* (Holotype: LE, photo GH!).

DESCRIPTION

Plants frequently growing in dense clusters, or single, farinose in youth, becoming more or less efarinose in age. Scape (1)2-10 cm high. Leaves including petiole 1-2 (3.5) cm long, 0.1-0.7 cm wide, spathulate, elliptical, or rhombic, crenate to remotely denticulate. Involucral bracts gibbous or saccate at base, involute above, 0.2-0.5 cm long. Umbel (1)3-8 (12) flowered. Pedicels 0.2-0.8 cm long, erect or spreading but not capillary. Flowers distylous. Calyx campanulate, green or with purple striations, ca 0.3 cm long, obscurely ribbed, divided up to 1/2 its length with lanceolate teeth covered with capitate glands. Corolla lavender, rarely white, throat yellow; tube 0.6-0.8 cm long, at anthesis 1.5 times length of the calyx; limb (0.8)1-1.5 cm wide, lobes slightly or deeply emarginate. Stamens ca 1 mm long, anthers located near middle of the corolla tube in pin plants. Stigma capitate, in pin plants located at or just above the annulus. Positions reciprocal in thrum plants.

Pollen dimorphic, ca 13 μm in diameter in pin plants, ca 17 μm in thrum plants; exine microreticulate, 3-syncolpate. Seeds strongly reticulate, ca 0.5 mm long. Chromosome number $2n = 36$ (Alaska: *Kelso 84-115, 83-292* at ALA; Johnson and Packer 1968. Northeast Siberia: Zhukova 1965, 1966, 1982; Zhukova & Tikhonova 1971, 1973). $2n = 18$ (Alaska: Thomas 1951; Siberia: Zhukova 1980; Zhukova & Petrovsky 1980: q.v. *P. mistassinica* here).

Habitat: In halophytic grass, sedge and herb wet meadows along the coast; associated species: *Carex ramenskii Kom., Carex rariflora* (Wahlenb.)Sm., *Carex subspathacea* Wormskj., *Rhodiola integrifolia* (Raf.), *Deschampsia caespitosa* L., *Leymus mollis* (Trin.)Pilger, *Potentilla egedii* Wormskj., *Saxifraga hirculus* L..

Range: In North America from the Bering Sea coast to Cape Bathurst in the Northwest Territories. Total range in Asia uncertain, but clearly present in coastal regions from the Chukotsk Peninsula to the Kolyma River (Fig. 2.6).

Representative specimens examined.

CANADA. NORTHWEST TERRITORIES. Anderson River: *Barry 218, 67, 290, 291, 337* (DAO); Cape Bathurst: *Anderson 6 Jul 1912* (NY), *Johanson 533* (BM, NY); Cape Parry: *Scotter and Zoltai 25998* (DAO); Hanson Harbor: *Scotter 10269* (DAO); MacKenzie River Delta: *Cody and Ferguson 9996* (DAO); Richards Island: *Erickson in 1972* (UBC), *Porsild 7450* (COLO); Tuktoyaktuk Peninsula: *Kuk in Jun 1969* (CAN), *Owen and Hanson 744217* (DAO), *Parmelee 2565* (DAO, UBC), *Pearson et al. 74112* (DAO); *Robertson 119* (ISC). YUKON. Clarence Lagoon: *Cooper 236* (NY); Herschel Island: *Bird 2 Jul 1953* (DAO), *Cooper 26, 63C, 92, 148, 542* (NY), *Johanson 265* (CAN), *Wood 201* (CAN); Komakuk Beach: *Parmelee 2825* (DAO); Mackenzie River Delta: *Porsild 16843* (ALA, BM), *Porsild and Porsild 2266* (BM).

USA. ALASKA. Aleutian Islands, Unalaska: from herb. *Fischer without date* (NY, without accesson number); Arctic Ocean coast, Barter Island: *Barkalow P18* (ISC), *Henry 55* (K), *Masik 657* (K), *Mason 248* (ALA), *Spetzman 1203* (ISC); Beaufort Lagoon: *Murray 3117* (ALA, COLO, DAO); Camden Bay: *Johanson 56* (BM, NY), *Johanson 28834* (GH); Cape Beaufort: *Hultén 3-7 Aug 1961* (ALA, CAS, NY), *Stone 1146* (CAS); Harrison Bay: *Lipkin and Dawe 867* (ALA); Icy

Cape: *Keller 1250* (ALA), *Lehnhausen and Quinlan 42* (ALA); Navagapak Point: *Argus and Chunys 5930* (GH); Prudhoe Bay: *Kokhryakov et al. 6743* (ALA), *Marris 19660, 19926* (BM), *Mason 113* (ALA), *Murray 77-20* (ALA), *Raynolds in Jun 1984* (ALA), *Walker 84-38, 517* (ALA), *Walker and Palmer 80A-19, 80A-52* (ALA). Bering Sea Coast, Chevak: *Boise and Wood 7807* (ALA), *Boise 006* (ALA); Dowry Creek: *Williams 3510* (ALA); Goodnews Bay: *Lloyd in 1935* (ISC); Hooper Bay: *Stewart 241* (NY); Igiak Bay: *Blurton Jones 24* (ALA); Pastolic: *Dall 25 Jun 1871* (NY), *Porsild and Porsild 1014* (GH); Qiqertariaq: *Porsild and Porsild 1091* (GH); Scammon Bay: *Hultén 26 Jun 1961* (ALA, CAS, US); Sheeshalik: *Heller 124* ; St. Michael: *Bannister in 1865-1866* (GH); Unalakleet: *Anderson 3295* (ISC). Bering Sea Islands, Nunivak Island: *Macoun 101405* (CAS), *201* (GH), *Utermohle 180* (ALA); St. Lawrence Island: *Geist in 1931* (ALA, CAN, GH, K, NY), *Kjellmann in 1879* (K), *Mason 6086* (CAN, CAS, K, NY), *Mason 10 July 1931* (K, NY, US), *Rausch and Fay 450* (CAS), *Sauer 28 Jun 1960* (CAN), *Young 67, 213, 426, 477* (GH). Chukchi Sea Coast, Cape Dyer: *Viereck and Bucknell 4039* (ALA, COLO); Cape Espenberg: *Racine 117* (ALA); Cape Lisburne: *Anderson 4546* (ISC); Cape Thompson: *Belson 92* (ALA), *Wood and Wood 568A* (ALA); Kitluk River: *Ward 4* (ALA); Kivalina: *Bucknell 34* (ALA); Kotzebue: *Anderson 4755B* (ISC), *Heller 113* (ISC), *Mertens ex. herb. Acad. Petrop.* (NY), *Pegau 14-70* (ALA), *Scammon 40618* (GH), *Welsh 5723* (ALA), *5839B* (ISC), *Williams 1686B* (BM); Kotzebue Sound: *Beechey s.n.* (K), *Lay and Collie in 1847* (BM); Kukpowruk River: *Chambers 76* (CAS); Ogoturok Creek: *Hultén in 1961, Johnson and Neiland 39, 52* (ALA), *Johnson et al. 67, 186* (ALA, DAO), *Packer 1884* (DAO); Pitmegea River: *Cantlon and Gillis 57-210* (ALA), *Shetler and Stone 3171* (ALA); Point Hope: *Anderson 3813* (ISC), *Corwin crew in 1881* (GH), *Hutchinson 696-701* (K), *Rasmussen 1341* (CAN), *Stewart 334* (NY),*Welsh 3831* (ISC, NY),*Williams 3464* (ALA); Point Lay: *Anderson 4473* (ISC). Seward Peninsula, Brevig Lagoon: *Kaufman 85-3* (ALA); Cape Espenberg: *Racine 117* (ALA); Church Rock: *Zachel in 1983* (ALA); Deering: *Anderson 4836* (ISC); Imuruk Basin, Canyon Creek: *Zachel 21 Jun 1983* (ALA); Nome: *Chambers 76* (CAS), *Hultén 1040* (ALA), *Reat in 1944* (K), *Williams 707* (ISC); Nome River mouth: *Kelso 83-164* (ALA), *Thornton 2243* (K), *Williams 478* (CAS); Port Clarence: *Kjellman in 1879* (K), *Mason 19 July*

1931 (K, US); Safety: *Kelso 84-11* (ALA),*Walker in 1970* (ALA); Shishmaref: *Rynning 1027* (ALA); Teller: *Anderson 3594* (ISC), *Scammon 5590, 5591* (GH); Wales: *Kelso 81-180, 82-192, Kelso et al. 180* (ALA, COLO, NY), *Mason 76194* (ALA).

USSR. SIBERIA. Arakamtchechene Island: *Wright in 1853-1856* (K, NY, US). Chukotsk Peninsula, Cape Chapline: *Tasarin 21 Jul 1957* (DAO); Chaplinski Hot Springs: *Tavriliov 14 Jun 1957* (DAO). Pitlekaj: *Kjellman in 1879* (K). Plover Bay: *Coville and Kearney in 1844* (BM, CAS, GH, K, NY), *Macoun 109* (NY), *202* (CAN, GH).

DISCUSSION

The first collection of the then unnamed species *P. borealis* was in 1805 by Langsdorff, naturalist with the Krusenstern expedition during its attempt at a global circumnavigation. The expedition went no further north than the Pribilof Islands (Hultén 1940), so the collection of *P. borealis* must have been made somewhere in the southern Bering Sea region. The plants collected by Langsdorff were given to Fischer at Leningrad and duplicates sent to Kew and Edinburgh as *P. araboides* with the name of Fischer rather than Langsdorff attached (Smith and Fletcher 1943).

In 1816-17, Chamisso and Eschscholtz travelled through the Bering Strait with the Kotzebue expedition, collecting at Unalaska, St. Lawrence Bay (Chukotka), St. Lawrence Island, and Shishmaref on the Seward Peninsula of Alaska. Later, Chamisso and Schlechtendal (1826) described the plants from this expedition, giving the name *P. mistassinica* (after a species just then described from Canada) to several specimens they collected from the Bering Strait area.

In 1844, *Primula borealis* was formally described by Duby who based the species on the collections of Chamisso from western Alaska. Bunge is also listed as a collector of type material of *P. borealis*, but this cannot be correct since he never visited the area. Duby was probably referring to material from herb. Bunge that was actually collected by Langsdorff or Chamisso and Eschscholtz. At the same time, he described a second species, *P. parvifolia*, based on the early Fischer material collected by Langsdorff somewhere in the Bering Sea region.

The diagnoses provided by Duby in his conspectus of the genus *Primula* were very brief. *Primula parvifolia* and *P. borealis* differed primarily in leaf morphology, and the species were of dubious distinction to the other botanists of the

day. Ledebour (1847) reviewed the collections of Chamisso and reduced *P. parvifolia* to a synonym of *P. borealis*. Pax (1889) briefly put both *P. parvifolia* and *P. borealis* under the Eurasiatic *P. farinosa,* but later (1905) restored *P. borealis* to a species and made *P. parvifolia* a variety.

In 1898, Small described *P. tenuis* from the Yukon delta in Alaska. He noted a resemblance to *P. borealis*, but distinguished his new species by its "flimsy leaves, shorter pedicels, turbinate calyx lobes, and narrow segments...the corolla tube is further exserted than in *P. borealis* and the more delicate lobes less deeply notched".

Busch (1926) ignored *P. parvifolia* and *P. tenuis* altogether, annotated her version of *P. borealis*, and added two new taxa from the Bering Strait region: *Primula chamissonis* and *P. ajanensis* . *Primula chamissonis* was based on material collected by Chamisso and Eschscholtz near Kotzebue, Alaska, and was distinguished from *P. borealis* by its greater height, longer pedicels, and fewer flowers. *Primula ajanensis* was described from the Ajan Mountains in Siberia along the Sea of Ochotsk and was distinguished by dense yellow farina on the underside of the leaves. It otherwise resembled *P. borealis* .

In 1928 Fernald reviewed section *Farinosae* (now called section *Aleuritia)* in North America. He subsumed the names *P. chamissonis* and *P. tenuis* under *P. borealis*, but separated a taxon from the Seward Peninsula that was distinguished by its plane bracts and small corolla. He applied the name *P. parvifolia* incorrectly to this species, which we now recognize as as an endemic of the Seward Peninsula under the name *P. anvilensis* (Kelso 1987a). Fernald also recognized *P. ajanensis* and expanded its range to Alaska based on a specimen from Nunivak Island in Alaska (*Macoun 8 Aug 1891,* CAN! GH!) that was heavily farinose on the lower leaf surfaces. Hultén (1948) did not agree with Fernald that *P. ajanensis* occurred in Alaska. Unlike Fernald, he had seen the variability in *P. borealis* in the field and preferred to include the farinose individuals from the Bering Sea region under that name.

Smith and Fletcher (1943) reviewed *P. borealis* and its synonyms. They agreed with Hultén that the species was polymorphic in its vegetative characteristics, and particularly so with regard to the amount of farina present. It was, however, consistently marked by large corollas on short pedicels subtended by saccate bracts. Smith and Fletcher recognized the names *P. parvifolia* (sensu Duby non Fernald),

P. tenuis, and *P. chamissonis* as synonyms of *P. borealis*. They compared the nomenclature of the primulas in the Bering Strait region with those of the North Pacific islands of Japan and the Asiatic coast along the Sea of Ochotsk, making *P. ajanensis* a synonym of the Japanese taxon *P. matsumurae* Petim. *Primula ajanensis* is currently treated as *P. modesta* Biss. & Moore var. *matsumurae* (Petim.) Takeda in contemporary Japanese floras (cf. Ohwi 1965; Ito 1981, 1982; Shimizu 1983).

My examination of the abundant material of *P. borealis* now available supports the conclusions of Hultén and Smith and Fletcher that the species is extremely variable in height, leaf morphology, and amount of farina present. All of these characters can be influenced by ecological and phenological factors. Sand dune populations of *P. borealis* contain individuals less than 2 cm tall, whereas populations growing in more stable, nutrient-rich sites can contain plants over 10 cm in height. These robust individuals (for example, *Welsh 5839A, Welsh 5723*, ISC!) are similar to what Busch described as *P. chamissonis*. Leaf length increases over a growing season, and, as with other members of section *Aleuritia*, the amount of farina present is to a great extent age dependent. Young leaves are heavily farinose, but later in the summer only a few traces remain.

Primula borealis is consistent in its floral characteristics. The wide corolla limb plus the full symmetrical umbel and short pedicels on top of a short scape make the plants appear top-heavy at anthesis. Individuals growing in environmentally stressed areas such as windy beach fronts, often have depauperate umbels with fewer flowers. The specimens described by Small as *P. tenuis* are typical of this growth form. In all specimens, the involucral bracts are consistently saccate or gibbous in life, although this character can sometimes be difficult to detect in poorly pressed herbarium material. *Primula borealis* is always found in saline environments and is particularly common in sand dunes and estuarine marshes in soil that is continually damp but not saturated. It is often sympatric with *Primula nutans*, and herbarium sheets frequently contain both species. *Primula nutans* is easily distinguished from *P. borealis* by its ovate, petiolate leaves and auriculate bracts. The collection of *P. borealis* from the interior Yukon Territory reported in Porsild (1966) and Porsild and Cody (1980) was based on a misidentification of *P. mistassinica*. Because of a lack of specimens available for inspection, the range of *P. borealis* in Siberia beyond the coast of Chukotka is unclear. Soviet literature

(Yurtsev et al. 1979; Tolmatchev and Yurtsev 1980; Kozhevnikov 1981) reports the species as far west as the Lena River. However, the chromosome number attributed to *P. borealis* there (Zhukova and Petrovsky 1980) is diploid, $2n = 18$, rather than the tetraploid given in numerous other counts. The Eurasiatic taxon *P. farinosa L.*, a diploid, can resemble *P. borealis* closely. It is found throughout northern Siberia, including the Lena River basin, and it is likely there has been some confusion between the two species there. Consequently, I hesitate to accept the conclusion of Smith and Fletcher (1943) that the taxon *P. stricta* var. *jacutenis* Busch from the Yakutsk region of Siberia is entirely synonymous with *P. borealis*. They are certainly correct that it is not any form of *P. stricta*. However, I suggest that the specimens named by Busch from the mountainous region along the Lena River, and the specimens identified as *P. borealis* from the Anyui Mountains with the diploid chromosome number reported by Zhukova and Petrovsky (1980) might be more properly allied with *P. farinosa* than with *P. borealis*.

South of the Chukotsk Peninsula, it is difficult to separate the range of the North Pacific species *P. modesta* (including var. *matsumurae* (Petim.)Takeda and var. *fauriae* (Franch.)Takeda from that of *P. borealis*. No recent systematic work has been done on the Asiatic members of section *Aleuritia*, but there is a clear affinity between *P. borealis* and *P. modesta* s.lat. in their large flowers, symmetrical umbels, and rhomboid leaves. *Primula modesta* is known to be diploid (Shimizu 1982) and the other diploid chromosome counts reported for *P. borealis* in Siberia are from mountainous regions along the Sea of Ochotsk (Yurtsev et al. 1979), near the range of *P. modesta*.. It seems reasonable to consider that the lower chromosome numbers attributed to *P. borealis* in this region are applicable instead to one of the varieties of *P. modesta*.

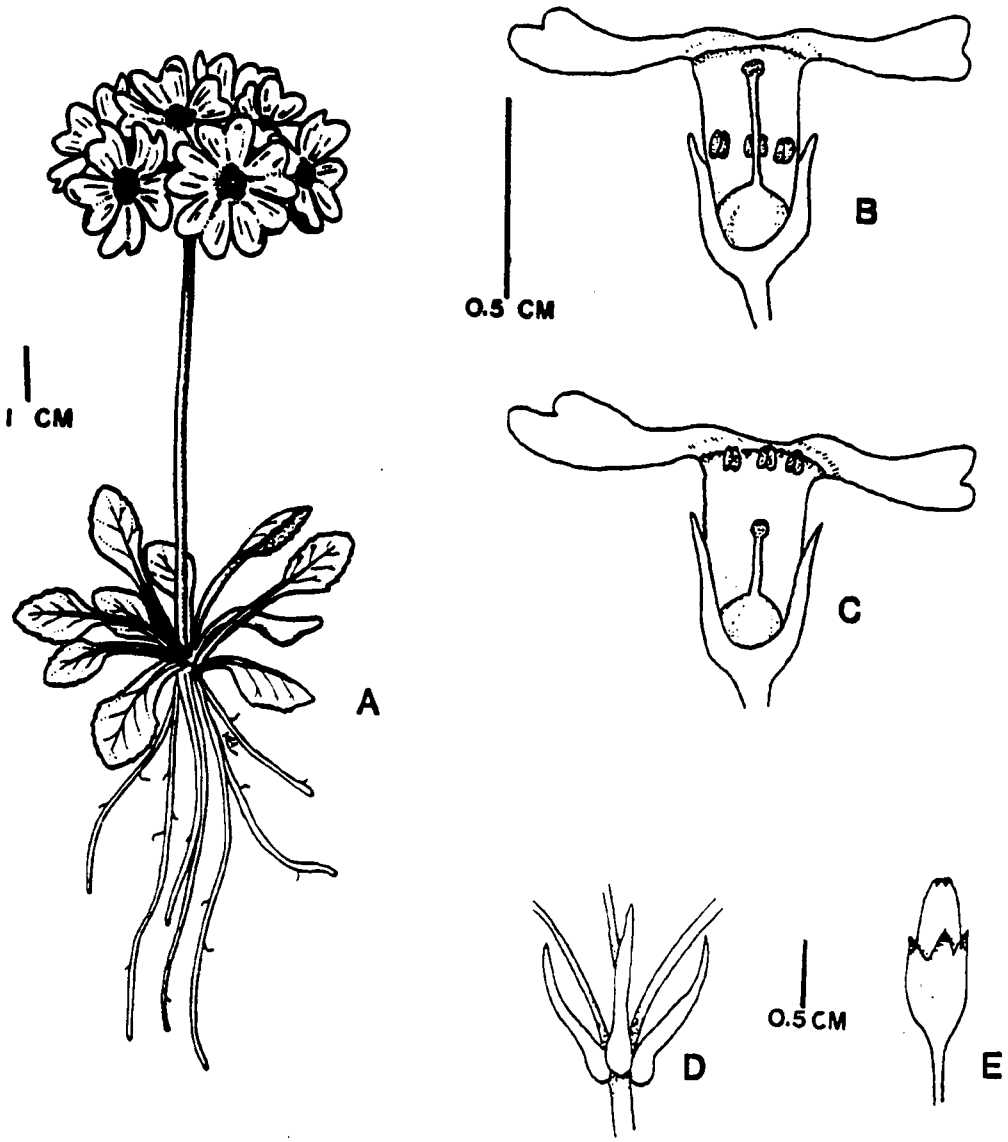


Fig. 2.5. *Primula borealis*. A. Habit. B. Pin flower. C. Thrum flower. D. Bracts. E. Capsule.

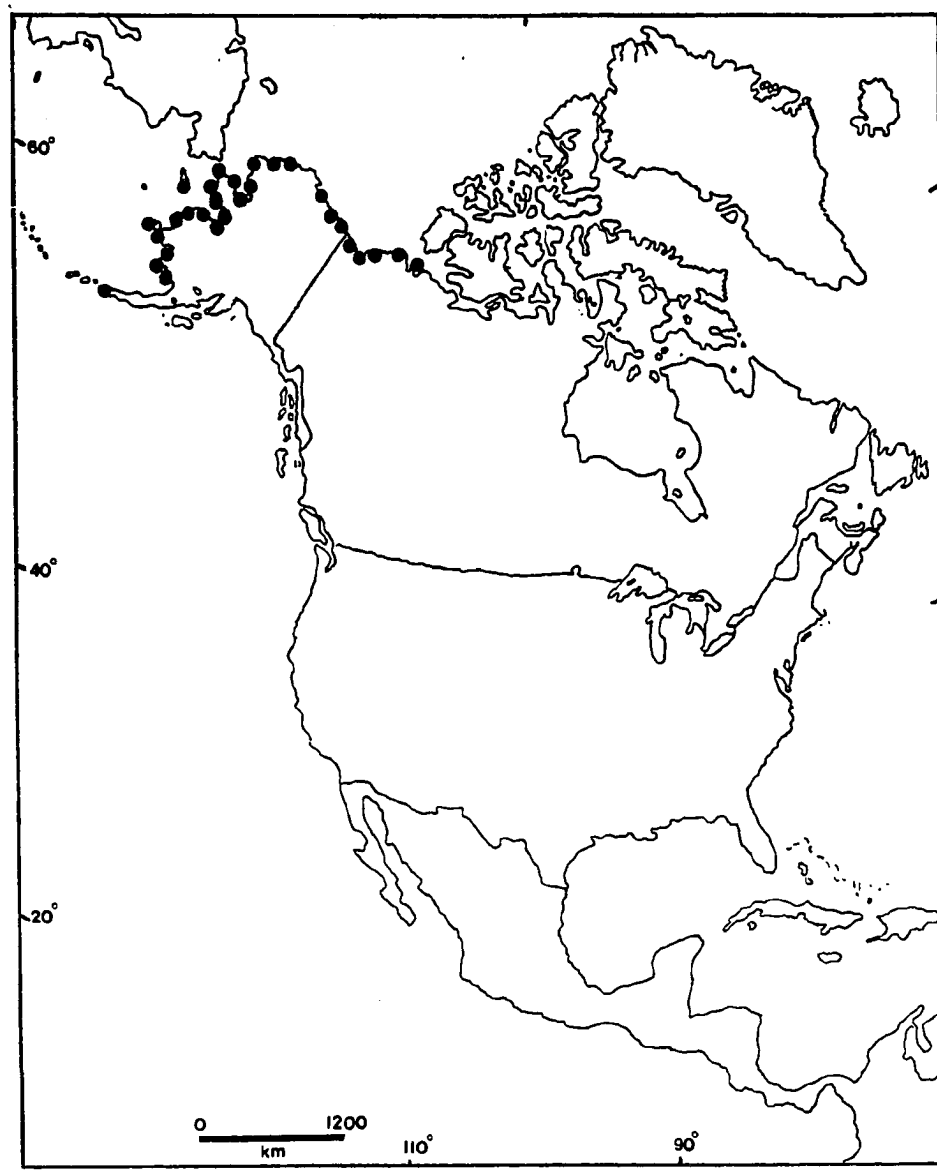


Fig. 2.6. Known range of *Primula borealis* in North America.

Primula incana M.E. Jones (Fig. 2.7)

Primula incana Jones, Proc. Cal. Acad. 5: 706. 1895. *P. farinosa* var. *incana* (Jones) Fernald, Rhodora 9: 16. 1907. *P. farinosa* subsp. *incana* (Jones) Smith and Forrest, Notes Roy. Bot. Garden Edinburgh 16: 24. 1928. TYPE: UNITED STATES. UTAH. Tropic. *Jones 5312*. (Holotype: RSA!)

Primula americana Rydb., Bull. Torrey Bot. Club 28: 500. 1901. TYPE: UNITED STATES. MONTANA. Deer Lodge. *Rydberg 2746* (Holotype: NY!)

DESCRIPTION

Plants slender, tall, and heavily farinose, occasionally efarinose. Scape to 46 cm high. Leaves elliptic or oblanceolate, including the petioles to 6 cm long, blade 0.3-1.6 cm wide, margins denticulate, blade gradually narrowing onto a broadly winged petiole. Involucral bracts oblong, densely covered with white farina, flat above, saccate or gibbous at the base, 0.5-1 cm long. Umbels capitate, (4)7-19 flowered, pedicels short, 0.3-0.9 cm long. Flowers homostylous. Calyx green, heavily farinose, cylindrical, obscurely ribbed, 0.4-0.7(1) cm long, divided up to one third its length by lanceolate teeth covered with capitate 3-4 celled glands. Corolla lavender with yellow throat; limb 0.4-0.8 cm wide, tube equal to or slightly longer than calyx, limb emarginate. Stamens ca 1 mm long, located in upper portion of corolla tube. Stigma capitate, located adjacent to anthers. Pollen ca 19 μm diam., exine microreticulate, 4-syncolpate. Capsule cylindrical to slightly elliptical, 0.2-0.3 cm wide, 1.5-2 times the length of the calyx. Seeds brown, reticulate, ca 0.2 mm long. Chromosome number: $2n = 54$ (Alaska: *Kelso 83-350, 84-53, 84-91;* Yukon: *Kelso and Holmes 84-37,* all at ALA). $2n =$ c. 50 (Colorado:*Wittmann and Wittmann 2542,* at ALA). $2n = 72$ (Colorado: Vogelmann 1960).

Habitat: In seral herb communities with alkaline clay soil in river flood plains and in open meadows; associated species in Alaska: *Carex aurea* Nutt, *Carex krausei*

Boeck., *Hordeum jubatum* L., *Parnassia palustris* L.; in Colorado found growing with *Primula egaliksensis* Wormskj.

Range: Rare in southern Utah, Colorado, Wyoming, and Montana, more common in Canada from British Columbia east to western Manitoba, rare in the Yukon and Alaska (Fig. 2.8)

Representative specimens examined.

CANADA. ALBERTA. Banff: *McCalla 2422* (K); Calgary: *Malte and Watson 1278* (COLO); Craigmyle: *AHB 432* (E, K), *Brinckman 5153* (DAO); Cypress Hills: *Cormack 17* (DAO), *Macoun 5313* (E), *de Vries 2031* (DAO); Delia: *Boivin and Perron 12414* (DAO); Edson: *Groh 1 July 1935* (DAO); Fort Fitzgerald: *Cody and Loan 4700* (DAO); Fort Saskatchewan:*Turner 17* (DAO); Fort Smith: *Cody 13695* (DAO),*Wallis 9 Jun 1950* (DAO); Fort Vermilion: *Moss 9430* (DAO); Jasper: *Longfield and Blezard 185* (BM); Maligne Lake: *Scammon 2673* (GH); North Cooking Lake: *Goode 38B* (BM); Red Deer: *Fletcher 18 Jul 1904* (DAO); Rosedale: *Modie 942* (NY); Sunwapta River: *Porsild and Breitung 14521* (CAN), *Porsild 21322* (CAN); Vermilion: *Bird 18* (DAO). BRITISH COLUMBIA. Beatton River: *Raup and Correll 10059* (ALA); Tupper Creek: *Corran 10988* (GH). MANITOBA. Douglas: *Marshall 2* (DAO); Russell: *Dore and Lindsay 11250* (DAO); The Pas: *Krivda 2167* (BM, DAO). NORTHWEST TERRITORIES. Fort Norman: *Wynne Edwards 8563* (DAO); Fort Providence: *Thieret 4117* (DAO); Fort Smith: *Cody and Loan 3782* (BM, DAO), *3822, 4170* (DAO), *4573* (BM, COLO, DAO); Goodhope:*Wynne Edwards 8615* (CAN); Great Slave Lake: *Thieret and Rich 6000, 7633, 7661, 8265* (DAO); Lower Hay River: *Lewis 680* (DAO); Mackenzie Mountains: *Johnson and Munro 2229* (DAO); Mackenzie River: *Porsild 16681* (CAN); McMurray: *Smith 39* (K); Moose Jaw: *Macoun 1427* (BM); Norman Wells: *Cody 7810* (E), *Cody and Gutteridge 7344, 7358* (DAO), *7810* (ALA, BM, CAS, COLO, DAO), *Rigby 43* (BRY, ISC), *Shewell 108* (DAO); Slave River: *Reynolds 307* (DAO); Smith Creek: *Crickmay 2* (CAN); Yohin Lake: *Scotter 23457* (DAO). SASKATCHEWAN. Adamson: *Hudson 2528* (DAO); Adanae: *Boivin and Alex 10212* (DAO); Bell Lake: *Cox 1* (DAO); Beverly: *Looman 2575*

(DAO); Caron: *Ledingham 49-182* (DAO); Copeland: *Russell 3776* (DAO); Cypress Hills: *Breitung 5018, 5142, 5186* (DAO); Dunblane: *Bahrey and Russell S61073* (DAO); Emma Lake: *Russell on 7 Jul 1941* (DAO); Esterhazy: *Frankton 1407* (DAO); Greenstreet: *Groh 21 Jun 1933* (DAO); Hawken: *Russell and Simmons 18 Jun 1934* (DAO); Kindersley: *Jenkins 849* (DAO); Manor: *Boivin 8400* (DAO); McKague: *Breitung 9 Jun 1934* (DAO); Moose Jaw: *Macoun 12742* (K); Neda Lake: *Hudson 3138* (DAO); Prince Albert: *Bahrey and Russell 559136* (DAO), *Russell 54139* (DAO); Qu'Appelle Valley: *De Vries 830* (DAO); Regina: *Sheukenek 139* (DAO); Reserve: *Rowe 217* (DAO); Rosthern: *Heart 2* (DAO); Strawberry Lakes, Dry Lake: *Ledingham 3724* (DAO); Sutherland: *Ledingham 11 Jun 1934* (DAO); Swift Currant River: *Boivin and Perron 12093* (DAO); Ternan's Lake: *Jenkins s.n.* (DAO 365261); Tisdale: *Breitung 1752* (DAO); Webb: *Looman 12493* (DAO); Whitewood: *Boivin and Gillett 8538* (DAO); Worman: *Groh 20 Jun 1935* (DAO); Yorkton: *Russell 1292* (DAO).YUKON. Alaska Highway, Mile 951: *Welsh and Moore 7771* (ALA, BRY, COLO, ISC); Alsek River: *Raup and Raup 11922* (ALA, GH); Canol Rd.: *Porsild and Breitung 9670, 9784* (CAN), *10843* (CAN, US); Dezadeash River: *Scofield et al. 7367* (CAN), *Pearson 124* (CAN); Five Finger Rapids: *Tarleton 73* (US); Haines Junction: *Morton 2057* (CAN); Kaskawulsh River: *Pearson 67124A* (CAN); Kluane Lake: *Anderson 9356* (ISC), *Douglas and Douglas 6916* (CAN), *Kelso and Holmes 84-44, 84-37* (ALA), *Murray 353* (ALA), *Raup and Raup 12415* (ALA); Lewes River: *Gorman 1052* (CAN, US); Macintosh: *Schofield and Crum 7655* (UBC); Pine Creek: *Nowosad 51, 154* (DAO); Ross Park: *Porsild 1967* (CAN); Sulphur Lake: *Welsh and Moore 7778* (BRY); Twin Lakes: *R. Porsild 1866* (CAN); Whitehorse: *Porsild 9215* (CAN).

USA. ALASKA. Fairbanks: *Kelso 84-53, Kelso and Holmes 84-91, Kelso and Parker 83-350, Viereck 8025;* Fort Yukon: *Harms 3728;* Lower Gerstle River: *Spetzman 964;* Richardson Highway: *Porsild and Porsild 378* (GH). COLORADO. Clear Creek: *Ewan 14518, 14519* (CAS); Custer Co.: *Baltzell 100* (COLO); Fairplay: *Weber 13328* (COLO); Gunnison: *Baker 361* (BM, CAS, E, GH, NY), *Ripley and Barneby 7183;* Lake Co., 3 mi. NE Leadville: *Anderson 2545* (BRY); North Park: *Bessey 4213* (NY), *Denham 2121* (COLO), *Osterhout 3 Jul 1896*

(NY); Parkins: *Eastwood in Jul 1887* (COLO); South Park: *Cholewa 439* (NY), Goodman and Payson 2768 (CAS, NY), *Penland 1677* (NY), *Weber 5762* (CAS, COLO, DAO), *8761* (COLO); Wet Mountain: *Brandegee B378* (NY). MONTANA. Anaconda: *Blankinship 727* (BM, E); Armstead: *Payson and Payson 1735* (CAS, GH, NY); Deer Lodge: *Ripley and Barneby 8168* (CAS), *Rydberg 2746* (NY); Lina: *Shear 3068* (NY); Red Rock: *Shear 5042* (NY); Smith River, North Fork: *Scribner 143* (NY); Stinking Water Creek: *Porter 3 Jul 1871* (NY). UTAH. Escalante Mts.: *Goodrich 20720* (NY); Garfield Co., 21 mi from Escalante toward Henrieville: *Nixon 11337* (BRY); Uinta Mts, Sheep Creek Park: *Goodrich 19523* (BRY). WYOMING. Centennnial: *Brenckle 43060* (NY), *Porter and Porter 9976* (CAS), *Rollins 915* (GH, NY); Hanging Lake: *Packer 1970-113* (NY); Hams Fork and La Barge: *Curtis 13-21 Jul 1900* (NY); Jackson Hole: *Merrill and Wilcox s.n.* (GH); Little Laramie River: *Nelson 43* (NY),*187* (GH),*1961* (E),*3211* (K); Sublette Co.: *Payson and Payson 2648* (NY); Teton Co.: *Cholewa 375* (NY).

DISCUSSION

Primula incana is a generally well-marked and morphologically consistent species, with heavily farinose leaves, a tall scape, and flat bracts subtending tight umbels of small homostylous flowers. Many northern collections have been misidentified as the much smaller species *Primula stricta* because flowering begins when the scape is relatively short. Elongation of the scape continues throughout anthesis and pedicels elongate as seeds ripen. The characteristic tight umbels do not persist beyond anthesis, and individuals in fruiting stage may be many times taller than those in early flowering stage. While most plants are heavily farinose, some individuals in otherwise farinose populations, or entire populations, may be efarinose. As with other species in section *Aleuritia*, the farina is most apparent on young plants and lessens with age.

Primula incana is most similar to *P. laurentiana*. The latter species has a more eastern distribution, and is distinguished by larger flowers, longer pedicels, broader more denticulate leaves and involute rather than flat bracts. The ranges of the two species intersect near James Bay in Canada, and some specimens from this region are difficult to determine. *P. incana* has also been confused in the past with *P.*

alcalina , a white-flowered diploid species endemic to northern Idaho. Cholewa and Henderson (1984) have discussed the differences between the two taxa.

Cytologically, *Primula incana* appears to be a hexaploid. A single octoploid count has also been reported (Vogelmann 1956, 1960) from a population in South Park, Colorado, but I have recently obtained a hexaploid count (*Wittmann and Wittmann 2542* , $2n$ = ca 50) from the same population. The number of counts at the hexaploid level, and a lack of morphological differences beween the northern specimens and the southern ones suggest that the octoploid count may be an error. However, more counts are needed for *P. incana*, particularly from the regions between Alaska and Colorado.

Primula incana is known from southern Utah to the northern interior Alaska, and east through the prairie provinces to Manitoba. It is found in disturbed alkaline clay soil throughout its range. The type collection from Utah represents the southernmost population known; the label somewhat misleading reads "canyon above Tropic", although either the author or a later annotator corrected this to read "meadow". Other collections have been made from this area in recent years, although the exact type locality has not been found and the population may no longer exist (N. Holmgren, S. Welsh, pers. comm.). *Primula incana* is rare throughout Utah, Colorado, Wyoming, and Montana, but it becomes considerably more common in the Canadian prairie provinces. In the Yukon and Alaska, the species again becomes uncommon, and is limited to stable flood plains along rivers. The flood tolerance of this species was demonstrated by a population in Fairbanks that was flooded by the Tanana River in June of 1984 for several days during the height of flowering. Although plants were completely submerged, there was no evidence of damage to plants after the floodwaters receded, and seed set was abundant that year.

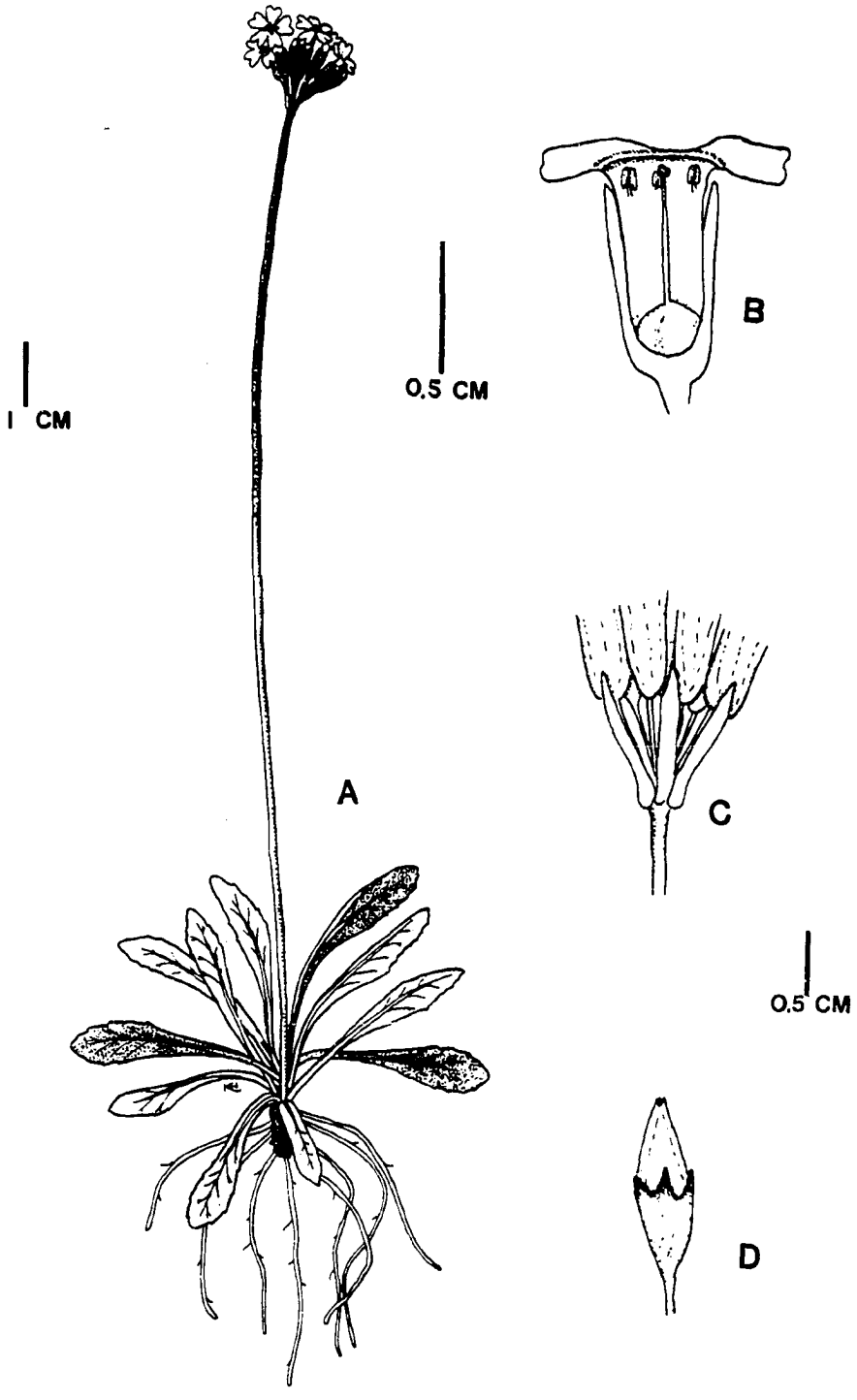


Fig. 2.7. *Primula incana*. A. Habit. B. Flower. C. Bracts. D. Capsule.

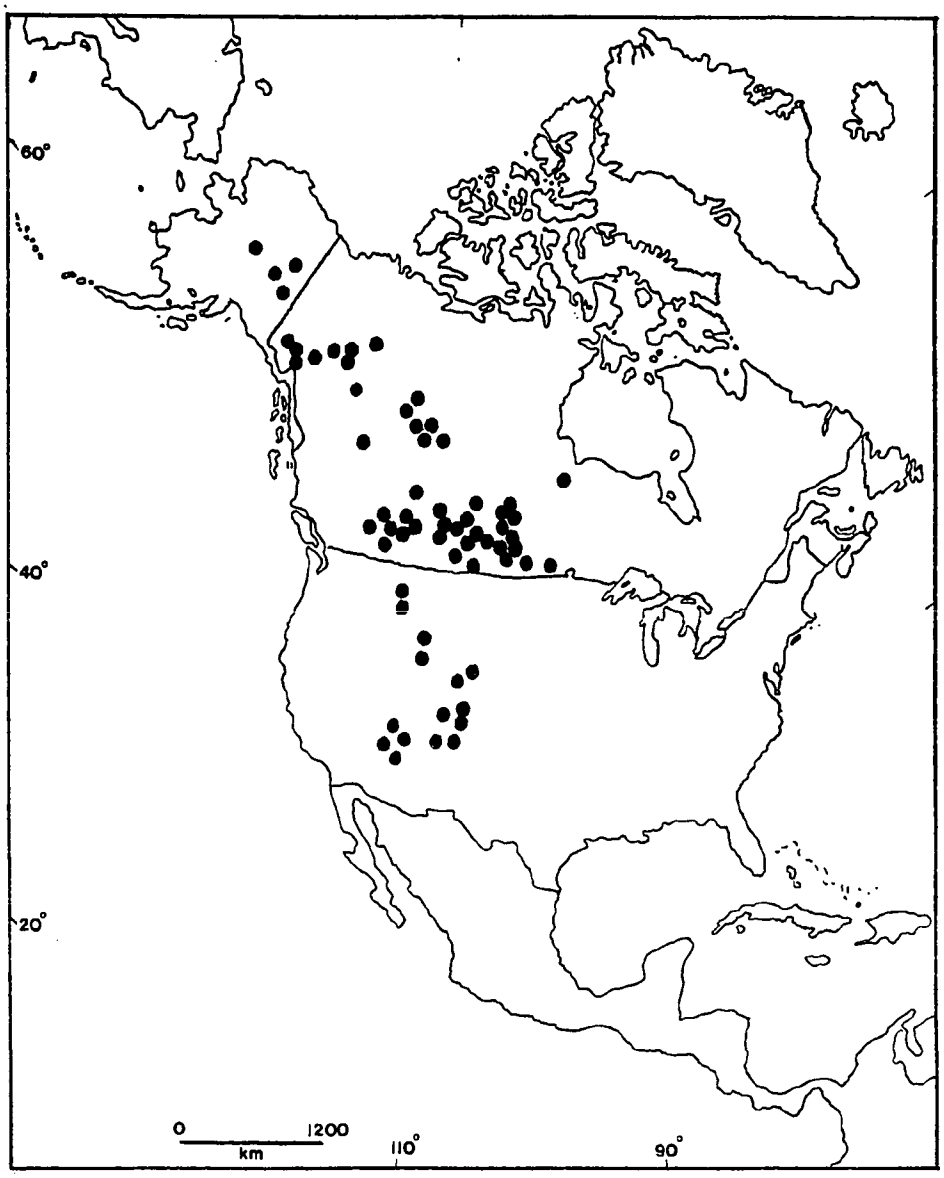


Fig. 2.8. Known range of *Primula incana*.

Primula laurentiana Fernald (Fig. 2.9)

Primula laurentiana Fernald, Rhodora 30: 68-72. 1928. *P. farinosa* L. var. *macropoda* Fernald, Rhodora 9: 16. 1907. *P. mistassinica* Michx. var. *macropoda* (Fernald) Boivin, Nat. Can. 93: 644. 1966. TYPE: CANADA. QUEBEC: Le Bic. *Fernald and Collins 243* (Holotype: GH)

DESCRIPTION

Plants farinose, glabrous. Scape 10-30(48) cm high. Leaves including petiole 3-10 cm long, oblanceolate to spathulate, rounded or acute at the apex with crenate margins, blade 0.4-1.3 cm broad, gradually narrowing onto winged petioles, densely farinose below with white or cream-colored farina. Involucral bracts saccate at base, involute above. Umbel 3-12 flowered; pedicels up to 1 cm long, elongating greatly in fruit. Flowers homostylous. Calyx campanulate to tubular, green, obscurely ribbed, 0.5-0.8 cm long, divided up to 1/3 its length by lanceolate teeth, densely covered with capitate glands. Corolla lavender with a yellow throat, tube 0.6-0.9 cm long, 1.5-2 times the length of the calyx at anthesis; limb to 1.6 cm wide, lobes to 0.7 cm wide, emarginate. Stamens ca 1 mm long, anthers located adjacent to the stigma in the upper 1/3 of the corolla tube. Pollen ca 19 µm diam., exine microreticulate, 4-syncolpate. Capsule elliptical, up to 1 cm long, exserted from the calyx. Seeds brown, ca 0.3 mm long, reticulate. Chromosome number: $2n = 72$ (unknown location: Bruun 1938; Labrador and Quebec: Vogelmann 1956, 1960; Quebec: Gervais and Cayouette 1985). $2n = 54$ (Labrador: Vogelmann 1960).

Habitat: Open areas on limestone, along riverbanks; associated species in Maine: *Agrostis stolonifera* L., *Aster novi-belgi* L., *Campanula rotundifolia* L., *Carex canescens* L., *Euphrasia canadensis* Townsend, *Iris hookeri* Penny, *Lomatogonium rotatum* (L.) Fries, and *Sagina nodosa* (L.) Fenzl (Famous and Campbell 1984).

Range: Most common in the Gaspé Peninsula of Quebec and in limestone regions of western Newfoundland, infrequent in the west to Hudson Bay and in the south to

northeastern Maine (Fig. 2.10)

Representative specimens examined.

CANADA. LABRADOR. Barge Point: *Ekblaw 17 Jul 1913* (GH); Battle Harbor: *Potter and Brierley 3627* (GH); Indian Harbor: *Abbé and Hogg 500* (GH), *Bishop 508* (E), *Potter and Brierley 3631* (GH), *Robinson 102* (GH); Pointe aux Eskimaux: *St. John 15 Jun 1915* (GH); Pt. Manvers: *Potter and Brierley 3629* (GH), *Potter 7723* (GH); Seal Island: *Rouleau 2776* (GH). NEWFOUNDLAND. Canada Bay: *Donly 3* (DAO); Cap Bauld: *Soper 1946* (DAO), Englee: *Savile 2731* (DAO); Cape St. George: *Mackenzie and Griscom 11028* (GH); Flowers Cove: *Wallace 74* (GH); Gros Morne: *Barabé and Chabot 17 Jun 1940* (DAO), *Cinq Mars et al. 64952* (DAO); Humber District: *Rouleau 1090* (DAO),*1785, 2776* (DAO, E); Ingornachoix Bay: *Fernald and Wiegand 3887, 3885* (GH); Notre Dame Bay: *Fernald and Wiegand 6068, 6069* (GH); Port au Port: *Fernald and Wiegand 3886* (GH); St. Anthony: *Savile and Vaillancourt 1923, 1798, 1841, 1721* (DAO), *Wallace 14* (GH). NOVA SCOTIA. Long Island: *MacFarlane & Simpson 161* (DAO). ONTARIO. Kapiskau River: *Ringius et al. 1018, 1037* (DAO); Swan River: *Dutilly and Lepage 31680* (DAO). QUEBEC. Anticosti Island: *Adams in 1934, 1935* (DAO), *Bernier et al. 301.15* (DAO), *Duplessis & Lemieux 301.256* (DAO). Attawapiskat: *Dutilly and Lepage 16485* (DAO); Bellburns: *Rouleau and Bouchard 118* (DAO). Bic: *Marie-Victorin et al. 45694* (DAO), *Rousseau 24911, 26411, 26685* (DAO), *Wynne Edwards 4014* (E); Cap Chat: *Allyre 2997* (DAO), *Duhamel et al. 61-55* (DAO). Cap Enrage: *Rousseau 26531* (DAO); Cap Gaspé: *Marie-Victorin et al. 17643* (DAO); Eastmain River: *Lepage 33542* (DAO); Gaspé Peninsula: *Bell 3 Jun 1862* (DAO), *Cody 47-853* (DAO), *Gerardin et al. 4858* (DAO), *Mulligan & Beales 3126* (DAO); Harrington Harbor: *Wood 85* (DAO); Ile Bonaventure: *Marie-Victorin et al. 17642, 17644* (DAO); Isle aux Basques: *Cayouette 8078* (DAO); Ilet Canuel:*Champlain 630A* (DAO); James Bay: *Dutilly & Lepage 31.680* (DAO), *Ringius et al. 1037* (DAO), *Lepage 33.490* (DAO); Marsoui: *Cayouette and Ouattara 7399* (DAO); Metamek River: *Bowman in 1915* (GH); Matane Co.: *Lemieux 301, 8014* (DAO); Mount Louis: *Rousseau 31043* (DAO); Percé: *Adams 11 Aug 1935* (DAO); Point des Monts: *Cayouette S78155* (DAO); Sacré Coeur: *Raymond 25 Aug 1947* (DAO); Riviere Melezes: *Dutilly et al.*

28233 (DAO); Riviere aux Renards: *Marie-Victorin et al. 17320* (DAO); Saguenay Co.: *Hamel and Genenaux 3090B, 3592B* (DAO); Saint Simon: *Marie-Victorin et al. 44024* (DAO); Saint Fabien: *Rousseau 50017* (DAO); Tourelle: *Rousseau 31154* (DAO); Ungava Basin: *Dutilly & Lepage 39.116, 39.567* (DAO). USA. MAINE. Mt. Kineo: *Smith in 1866* (GH), *Kennedy 21 Sep 1887* (GH).

Primula laurentiana f. chlorophylla Fernald

P. laurentiana f. *chlorophylla* Fernald, Rhodora 30: 72. 1928. TYPE: CANADA. NEWFOUNDLAND. Dog Peninsula, St. Margaret Bay, *Fernald et al. 28913* (Holotype: GH!)

Representative specimens examined.

CANADA. NEWFOUNDLAND. Belle Isle: *Fernald et al. 26955, 26957* (GH), *Wiegand et al. 28908* (GH), *Wiegand and Hotchkiss 28904* (GH); St. Margaret Bay: *Fernald et al. 28913* (GH); St. John Bay: *Fernald et al. 28911* (GH). QUEBEC. Riviere Galiote: *Rousseau 52,363* (GH).

DISCUSSION

Along with most of the other North American representatives of section *Aleuritia*, *P. laurentiana* was initially treated as a variant of the wide-ranging European species *P. farinosa* L. (Fernald 1907). Fernald later (1928) recognized it as a distinct species and distinguished it from the American species *P. mistassinica* Michx. by its copious leaf farina, and by the taller and more robust scape. Unlike *Primula mistassinica,* which is diploid and consistently distylous, *P. laurentiana* is always homostylous, and it has an octoploid chromosome number, although a single hexaploid individual from Newfoundland has been reported by Vogelmann (1960). *P. laurentiana* is most similar to *P. incana* Jones. The latter species is also tall and heavily farinose but has much smaller flowers, flat rather than involute bracts, a more western distribution than *P. laurentiana,* and is a hexaploid. In central Ontario, however, the ranges of the two species intersect, and some individuals there have intermediate morphology.

Primula laurentiana is a pronounced calciphile with a distribution limited to eastern Canada and some scattered localities in northeastern Maine (Lewis 1983; Famous and Campbell 1984). It is particularly abundant along the coast of the Gaspé Peninsula in Quebec. The western extent of *P. laurentiana* may be limited by the presence of the acidic bedrock of the Canadian Shield west of Hudson Bay. The availability of alkaline soil, combined with a need for a cool summer temperature regime, probably influences the southern limit of the species. Cushman (1907) and Pike (1963) suggested that the presence of *P. laurentiana* on islands with acidic bedrock along the Maine coast is due to seed dispersal by birds where plants are able to become established in locally lime-rich soil from the whitewash used on lighthouses. Lewis (1983) suggested that an additional factor controlling these island distributions might be the need for well-drained sites with low competition and a basic substrate. These requirements are typical of all the species of *Primula* in section *Aleuritia*.

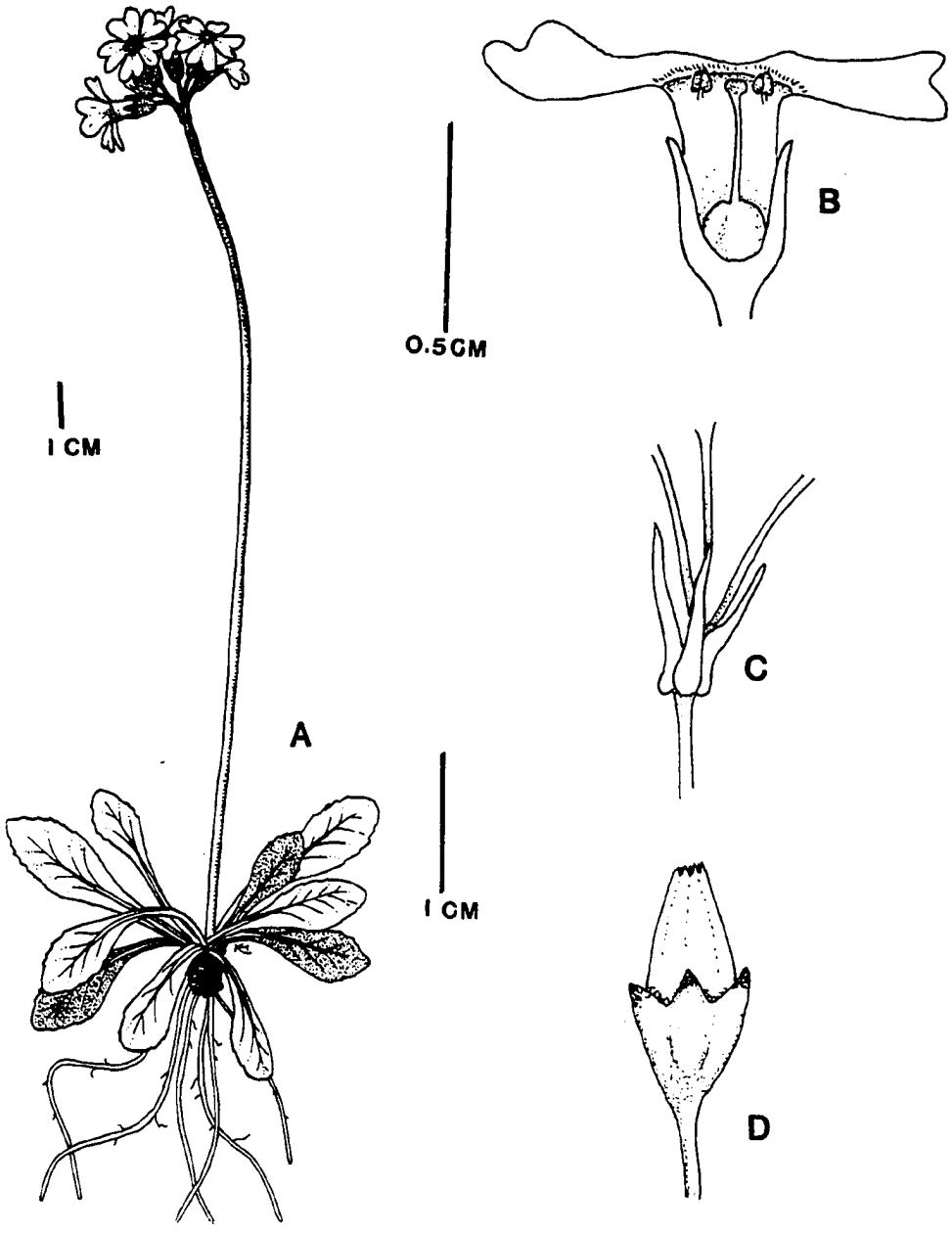


Fig. 2.9. *Primula laurentiana.* A. Habit. B. Flower. C. Bracts. D. Capsule.

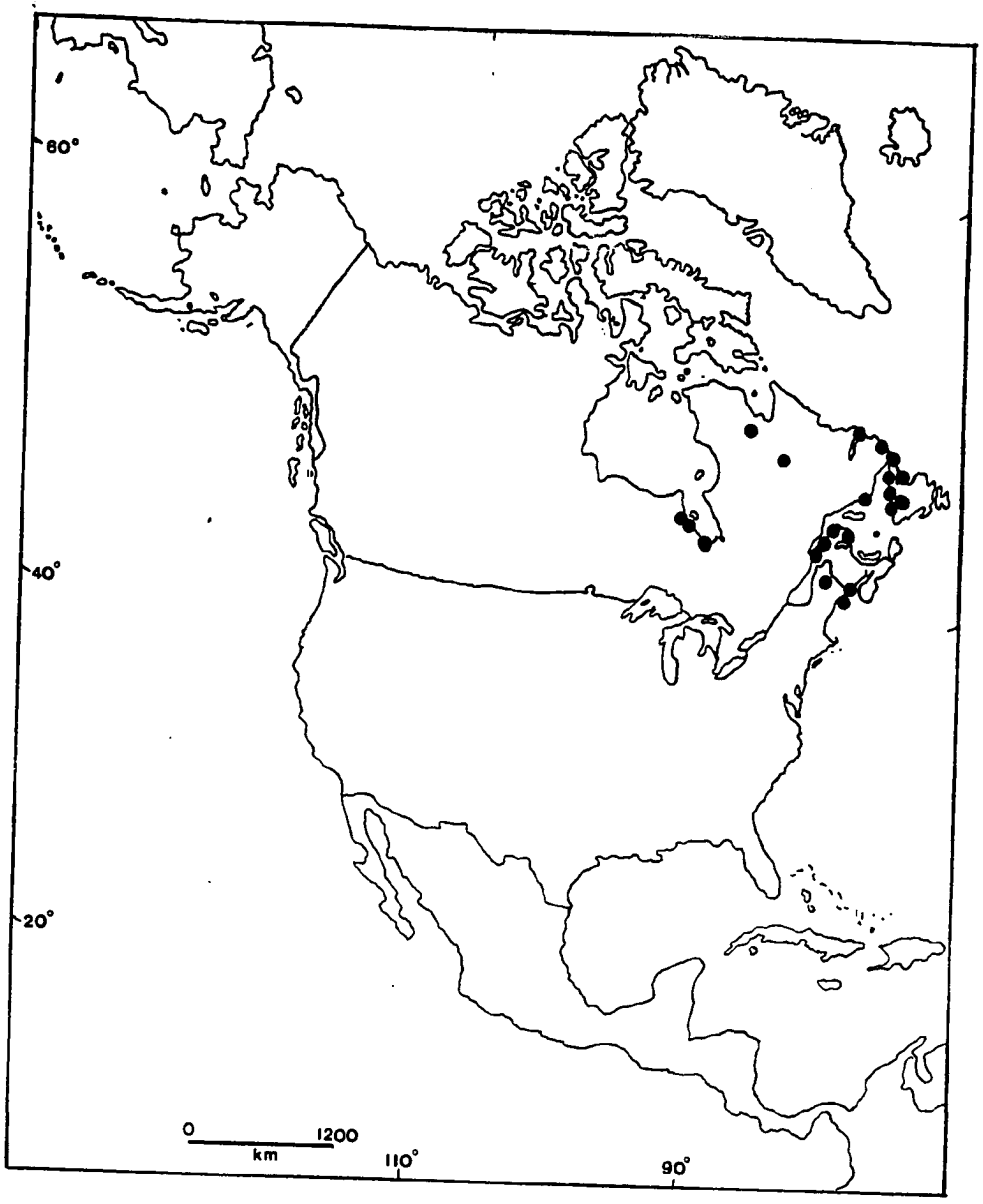


Fig. 2.10. Known range of *Primula laurentiana*.

Primula mistassinica Michaux (Fig. 2.11)

Primula mistassinica Michx., Flora Boreali-Americana 1:124. 1803. *P. farinosa* var. *mistassinica* (Michx.) Pax, in Engler, Bot. Jahrb. 10: 200. 1889. *P. farinosa* subsp. *mistassinica* (Michx.) Pax and Knuth in Engler, Das Pflanzenreich 4 (237): 85. 1905. *P. sibirica* var. *mistassinica* (Michx.) Kurtz in Engler, Bot. Jahrb. 19: 394. 1894.-pro parte. TYPE: CANADA. QUEBEC. Riviere des Goelands: Lake Mistassini. "Ad locus mistassins Canadam inter et fretum Hudsonis". *Michaux in 1792*. (Holotype: P)

P. maccalliana Wiegand, Bull. Torr. Bot. Club 27: 389. 1900. TYPE: CANADA. ALBERTA. Banff. *Maccalla 2433*. (Holotype: CU; isotype: K!)

DESCRIPTION

Plants usually efarinose, glabrous, sometimes with traces of farina on vegetative parts. Scape 5-15 cm tall. Leaves including the petiole 0.5-7 cm long, spathulate or elliptical, margins somewhat denticulate; blade 0.2-1.6 cm wide, gradually narrowing to winged petiole. Involucral bracts lanceolate, plane at base, 0.3-0.5 cm long, involute above, acute or somewhat obtuse at the tip. Umbel 1-5 (10) flowered. Pedicels 0.5-2.0 cm long, capillary. Flowers distylous. Calyx green or with purple striations, campanulate, obscurely ribbed, 0.3-0.5 cm long, divided up to 1/2 by lanceolate teeth sparsely covered with capitate glands. Corolla lavender with a yellow throat, sometimes white; tube 0.5-0.8 cm long, at anthesis 1.5-2 times the length of the calyx; limb 0.8-1.4 cm wide, lobes emarginate. Stamens ca 1 mm long, anthers located in pin plants in bottom third of corolla tube. Stigmas capitate, located in pin plants in upper third of corolla tube, positions reciprocal in thrum plants. Pollen dimorphic, in pin plants 9-11 µm diam., in thrum plants 13-15 µm diam.; exine microreticulate, 3-syncolpate. Seeds ca 0.5 mm long, reticulate. Chromosome number: $2n = 18$ (Yukon: *Kelso and Holmes 84-15* at ALA; Michigan, New York, Nova Scotia, Quebec: Vogelmann 1956, 1960).

Habitat: Open meadows and riverbanks, lakeshores, and around hot springs, in the southern portion of the range on cool, wet, north-facing slopes and cliff faces; calcareous substrates.

Range: Across boreal regions Alaska to Newfoundland, south to northern Vermont, New York, Illinois, Michigan, and Minnesota (Fig. 2.12).

Representative specimens examined

CANADA. ALBERTA. Banff: *Farr 583* (K), *McCalla 2433* (K), *Olgivie 18 Jul 1959* (UBC), *Ulke 231* (CAS); Bow River: *Bird 12905* (DAO), *Brunton et al. 1316* (DAO), *Mosquin and Seaborn 7002* (DAO); Jasper: *Jenkins 5929* (DAO), *Moss 4588* (UBC), *Porsild 22586* (CAN); North Saskatchewan River: *Boivin 4962* (DAO). BRITISH COLUMBIA. Al-Can Highway: *Beamish et al. 681136* (UBC); Cassiar District: *Rose 80348* (UBC); Kootenay Pk.: *Seel 53* (DAO); Liard Hot Springs: *Anderson and Brown 9911* (ISC), *Welsh and Moore 7393* (ISC). MANITOBA. Camperville: *Barton 5 Jun 1939* (DAO); Gillam: *Schofield 848* (BM, DAO, GH), *Wallis 2* (DAO); Mafeking: *Keleher 426* (DAO); Neepawa: *Krivda P-17* (DAO); Nelson River: *Scoggan 6372* (GH), *Tryon and Dahl 124* (COLO); Oak Lake: *Stukey 1* (DAO); Teulon: *Popowich May 1917* (DAO); The Pas: *Bryant 11 Jun 1954* (UBC). NEW BRUNSWICK. Mill Settlement: *Christie 7* (DAO); Restigouche River, *Chalmers 1428* (DAO), *Roberts and Bateman 64-3937* (DAO), *Rousseau and Bonin 32229* (DAO). NEWFOUNDLAND. Bonne Bay: *Fernald et al. 11950* (ISC); Corner Brook: *Rouleau 2714* (CAS, DAO, GH); Dayles Station: *English 6 Jun 1925* (DAO); Grand Falls: *Fernald and Wiegand 6070* (K); Harmon Air Force Base: *Bassett 254A* (DAO); Millerton Junction: *Fernald and Wiegand 6071* (BM); White Lake: *Rouleau 548, 2041, 2712* (DAO). NORTHWEST TERRITORIES. Carcajou Range, Mirror Lake: *Cody and Brigham 20399* (DAO); Florence Lake: *Cody and Brigham 20998* (DAO); Cartridge Hills: *Cody 18761* (DAO); Enterprise-MacKenzie River Highway: *Thieret and Rich 4616* (DAO); Great Bear River, *Porsild and Porsild 3321* (GH); Great Slave Lake: *Lewis 413* (DAO), *Raup 1225* (GH); James Bay, Charleton Island: *Porsild 4468* (GH); Lake Athabasca: *Raup 1228* (GH); Moose River: *Baldwin 1381* (GH); Mount Flett: *Cody and Spicer 11868* (DAO, UBC); Norman Wells: *Cody and Gutteridge 7645* (UBC, US); Poplar River: *Walker 2009* (DAO); South Nahanni River, Flat River Mineral Springs: *Scotter 3 July 1970* (DAO); Mackenzie Mountains: *Scotter 12452* (DAO); Virginia Falls: *Scotter 12494* (DAO); Tetcho Lake: *Rowe 1785* (DAO); Wrigley:

Shewell 4 (DAO). NOVA SCOTIA. Cheticamp River: *Smith et al. 7759* (DAO); Salmon River: *Mason et al. 24* (DAO), *Smith et al. 6382, 7906* (DAO); St. Paul Island: *Erskine 53,920* (DAO); Victoria City: *Smith et al 3750* (DAO). ONTARIO. Current River: *Jennings and Jennings 1662* (DAO); Grass Lake: *Jennings and Jenninings 1989* (DAO); Lake Superior: *Burgess 1201* (DAO), *Dore 9245* (DAO),*Garton 6213* (DAO); *Jennings and Jennings 2667* (DAO), *Moore 29 July 1961* (DAO), *Parmelee and Savile 3675* (DAO), *Voss 10457* (DAO); Moose Factory: *Savile and Spafford 64* (DAO); Moosonee: *Dickinson and Haber 553* (DAO); Nagagami River: *Moore 2013* (DAO); Picnic Lake: *Riley and Hoy 3109* (DAO); Rossport: *Jennings and Jennings 1166* (DAO); Thunder Bay: *Garton 1777, 2609, 2760, 2992, 4318, 4528, 4530, 7014, 7065, 7815, 9802* (DAO), *Hosie et al. 1867* (ISC), *Hutchinson 22* (DAO), *Macoun 69* (DAO), *McMorine in May 1881* (DAO), *Parmelee and Savile 3641* (DAO). QUEBEC. Anticosti Island: *Victorin 4296* (BM),*Vicorin and Germain 27243* (CAS); Chicoutimi: *Brisson 63131, 65194* (UBC); Chute aux Galets: *Brisson 65194* (COLO); Corner Brook: *Rouleau 548, 2714* (E); Lake Mistassini: *Rouleau and Rouleau 578* (BM, CAS, E, COLO); Lake Waconichi: *Jones 105* (BM); Rupert House: *Spafford 3* (DAO). SASKATCHEWAN. Amisk Lake: *Hudson 1494* (DAO); Carrot River Peak: *Hudson 3193* (DAO); Hasbala Lake: *Argus 1043-6* (DAO); Jan Lake: *Looman 11800* (DAO); Lake Athabaska: *Fredeen 127* (DAO); Lake La Ronge: *Ledingham 49-293* (DAO); Nipawim: *Breitung 5996* (DAO); Prince Alpert: *Ledingham 8 Jun 1937* (DAO). YUKON. Bonnet Plume Lake: *Butler and Olson 79* (CAN); Francis River: *Dawson 15844* (CAN); Wellesley Lake: *Spetzman 311* (CAN); White and Koidern Rivers: *Spetzman 312* (CAN); White River and Alaska Highway: *Kelso and Holmes 84-15* (ALA).

USA. ALASKA. Alaska Range:*Reed 2086* (CAS); Big River: *Drury 3802, 3874, 3949, 4120, 4231* (ALA, GH); Eli River:*Young 4231* (ALA); Kokrines Mts.: *Porsild and Porsild 679* (GH, ISC); Kugururok River: *Holmes 23 Jun 1984* (ALA); Kantishna Hills: *Smith and Reisland in June 1986* (ALA, Denali National Park Herbarium); Kuskokwim Mts.: *Dashevsky 20 Jun 1984* (ALA); Onion Portage: *Schweger 49* (ALA). ILLINOIS. Jo Daviess Co., Apple River Canyon: *Winterringer 7246* (DAO). MAINE. Aroostock Co.: *Fernald 82* (K). MICHIGAN. Charlevoix Co.: *Ries 93* (CAS); Douglas Lake: *Ehlers 6086* (CAS); Keewenaw Co., Devil's Washtub: *Farwell 12345* (DAO); Schoolcraft Co.: *Fernald and Pease 3477* (E); St.

Ignace: *Dore 21144* (DAO). MINNESOTA. Cook Co.: *Butters and Abbé 39* (DAO); Lake Superior: *Lakela 8023* (DAO); St. Louis Co.: *Lakela 19652* (DAO); Stillwater: *Peterson 22 May 1931* (DAO). VERMONT. Caledonia Co.: *Knowlton 578* (BM); Mt. Pisgah: *Pease s.n.* (GH); Sutton: *Knowlton 578* (CAS, COLO, DAO, K); Willoughby Mt.: *Eggleston 3289* (CAS), *31 May 1896* (DAO). WISCONSIN. Door Co.: *Bennett 2553* (BM).

***Primula mistassinica* f. *leucantha* Fernald**

Primula mistassinica f. *leucantha* Fernald, Rhodora 21: 148. 1919.

Differs only in the white corolla color. Found mixed with lavender morphs throughout the range, but particularly common in Newfoundland and Quebec.

***Primula mistassinica* var. *intercedens* (Fern.) Boivin**

Primula mistassinica var. *intercedens* (Fern.) Boivin, Nat. Canad. 93: 644. 1966.

P. intercedens Fern., Rhodora 30: 86-87. 1900. *P. mistassinica* f. *intercedens* (Fern.) J. Cayouette, Nat. Canad. 111: 443-445. 1984. TYPE: based on *P. farinosa* sensu Nuttall, Gen. 1:119. 1818, "calcareous gravel shores of the islands of Lake Huron around Michilimakinak, Bois Blanc, and St. Helena in the outlet of Lake Michigan", and *P. farinosa* var. *americana* Torrey, Fl. North. & Midl. U.S. 1: 213. 1824. "shores of Lake Huron, Lake Michigan, etc. *Douglass and Nuttall*". (Holotype: PH!).

Differs from var. *mistassinica* in the presence of dense yellow farina on the undersides of the leaves.

Range: Most common in the Great Lakes region, occasional in the Rocky Mountains, Alaska, and the Yukon.

***Primula mistassinica* var. *noveboracensis* Fernald**

Primula mistassinica var. *noveboracensis* Fernald, Rhodora 30: 19. 1928.

TYPE. UNITED STATES. NEW YORK. Triplehammer Falls, Fall Creek, Ithaca, *Eames 4804* (Holotype: GH!)

Differs from var. *mistassinica* only in the smaller flowers (0.8-1.0 mm wide) lacking a well-marked yellow throat.

Range: Throughout the southern part of the range.

DISCUSSION

Primula mistassinica has the broadest geographic range of all the North American species of *Primula* in section *Aleuritia*. Perhaps concommitantly, it is also one of the most polymorphic species. Fernald (1907) first placed the American taxon under the name *P. farinosa* L. after the widely distributed Eurasiatic taxon. In a later revision (1928), he examined the North American material more closely and concluded that it was completely distinct from *P. farinosa*. He recognized that *P. mistassinica* was variable in size, leaf shape, and flower color, and he included the Rocky Mountain taxon *P. maccalliana* under the name *P. mistassinica*. Fernald also added two infraspecific taxa: var. *noveboracensis*, which lacked a yellow eye in the throat of the corolla tube, and f. *leucantha* with a white corolla. He also described with hesitation a new species, *P. intercedens*, from the Great Lakes region based on a combination of early material collected by Nuttall and and his own observations. *Primula intercedens* differed from *P. mistassinica* only in the presence of a dense yellow farina on the undersides of the leaves and a more reticulate seed coat.

Infraspecific variation in *P. mistassinica* with particular reference to the questionable status of *P. intercedens* was examined by Vogelmann (1956). He concurred with Fernald about the polymorphic nature of *P. mistassinica*, and on the basis of interfertility of the morphs, identical cytology, and the abundance of intermediate forms, he subsumed *P. intercedens* under *P. mistassinica*. The yellow farinose morph has since been formalized as *P. mistassinica* var. *intercedens* by Boivin (1966).

Vogelmann recognized that there were some geographic trends in the morphological variation within *P. mistassinica*, which he attributed to a history of racial survival in isolated refugia during glacial episodes of the Pleistocene. However, the variation was continuous enough to preclude all but low level

infraspecific treatment. Vogelmann followed the nomenclature of Fernald and recognized var. *mistassinica,* var. *mistassinica* f. *leucantha,* and var. *noveboracensis.*

My examination of the abundant material of *P. mistassinica* now available leads me to agree with these authors that the taxon is variable in the vegetative characteristics of size, leaf morphology, and the amount of farina. It *is* consistent in habit, chromosome number, and floral morphology, and there is no justification to treat it as more than a single polymorphic species. Designation of infraspecific categories may be helpful for describing variation; however, in this instance they lack clear geographic coherence, intermediate forms are abundant, and it is often difficult to assign material to varietal level. In particular, var. *noveboracensis,* which lacks of a yellow throat, is particularly hard to distinguish on faded herbarium specimens. For these reasons, the infraspecific taxa within *P. mistassinica* are not elevated to subspecies, and the representative specimens listed above have been included under the general species description.

Primula mistassinica s. lat. is generally found in open meadows with a calcareous substrate, although in the warmer southern portion of the range it can be found on cool, wet, north-facing cliffs as well. Lake shores, hot springs, and disturbed areas along roadsides and streams are typical habitats elsewhere (cf. Porsild and Crum 1959, Soper et al. 1965, Porsild 1966, Fernald 1970). Because of the broad geographical range, the associated taxa vary considerably and the species can be found in numerous vegetation types (Scoggan 1950, Given and Soper 1981).

The range of *P. mistassinica* follows the boreal forest of North America. According to Vogelmann (1956), its southern limit generally follows the July 12° isotherm. In the northwestern portion of the range, *P. mistassinica* becomes increasingly rare and is recognized as threatened or endangered in several provinces (Douglas et al. 1981, Maher et al 1978, Maher et al. 1979, Straley et al. 1985). The western extent of *P. mistassinica* has been problematical. The species is very rare in the Yukon and Vogelmann (1960) suggested that it intergraded with *Primula borealis* there.

In northwestern Canada and Alaska *P. mistassinica* can be distinguished from other members of sect. *Aleuritia.* It is better represented by herbarium specimens than previously believed, although it should still be considered a rare species in northwestern North America. Many of the specimens from the continental

Northwest Territories and Yukon initially identified as *P. stricta* are in fact *P. mistassinica*. This is indicated by, among other attributes, their distylous flowers (*P. stricta* is consistently homostylous). Two populations from the interior Yukon (*Spetzman 311, 312*, DAO!), identified by Porsild (1966) as *P. borealis* are also *P. mistassinica*. *Primula mistassinica* differs from *P. borealis* in its more slender habit, plane involucral bracts, and fewer-flowered umbel on longer pedicels, as well as by the lower chromosome number which is reflected in the smaller pollen.

Hultén (1948) and Young (1976) recorded the presence of *P. mistassinica* in Alaska near the Yukon border. Examination of material from western Alaska has revealed several additional specimens that I have determined to be *P. mistassinica*. From the Brooks Range, *Schweger 49* and *Young 4321* (both at ALA), and *Holmes 23 Jun 1984* (ALA) have the few-flowered umbel, capillary pedicels, and plane bracts of *P. mistassinica*. An additional specimen, *Thomas 2245* (at CAS as *P. borealis*) from the Kukpowruk River near Point Lay is also *P. mistassinica*. The plants on this sheet are well into fruiting stage and therefore past the point when it is easiest to distinguish *P. mistassinica* from *P. borealis*. However, my determination of the specimen is supported by the diploid chromosome number obtained for the population (Thomas 1951) as well as its morphology. Several more specimens from southwestern and interior Alaska (*Drury 3802, 3874, 3949, 4120* at ALA, GH as *P. borealis* ; *Reed 2086* at CAS as *P. tschuktschorum; Dashevsky s.n. in 1984* at ALA, *Smith and Reisland 12 Jun 1986* at ALA and herbarium at Denali National Park, and *Porsild and Porsild 629* at GH, ISC) are also *P. mistassinica*. These are all small plants less than 6 cm in height, with small (less than 0.5 cm long) slightly farinose leaves, and few-flowered umbels. The Alaskan plants are identical to specimens of *P. mistassinica* from the continental Northwest Territories (*Cody and Brigham 20998, Simmons 116A, Marsh 5792*, all at DAO) and are well within the range of variation of the species.

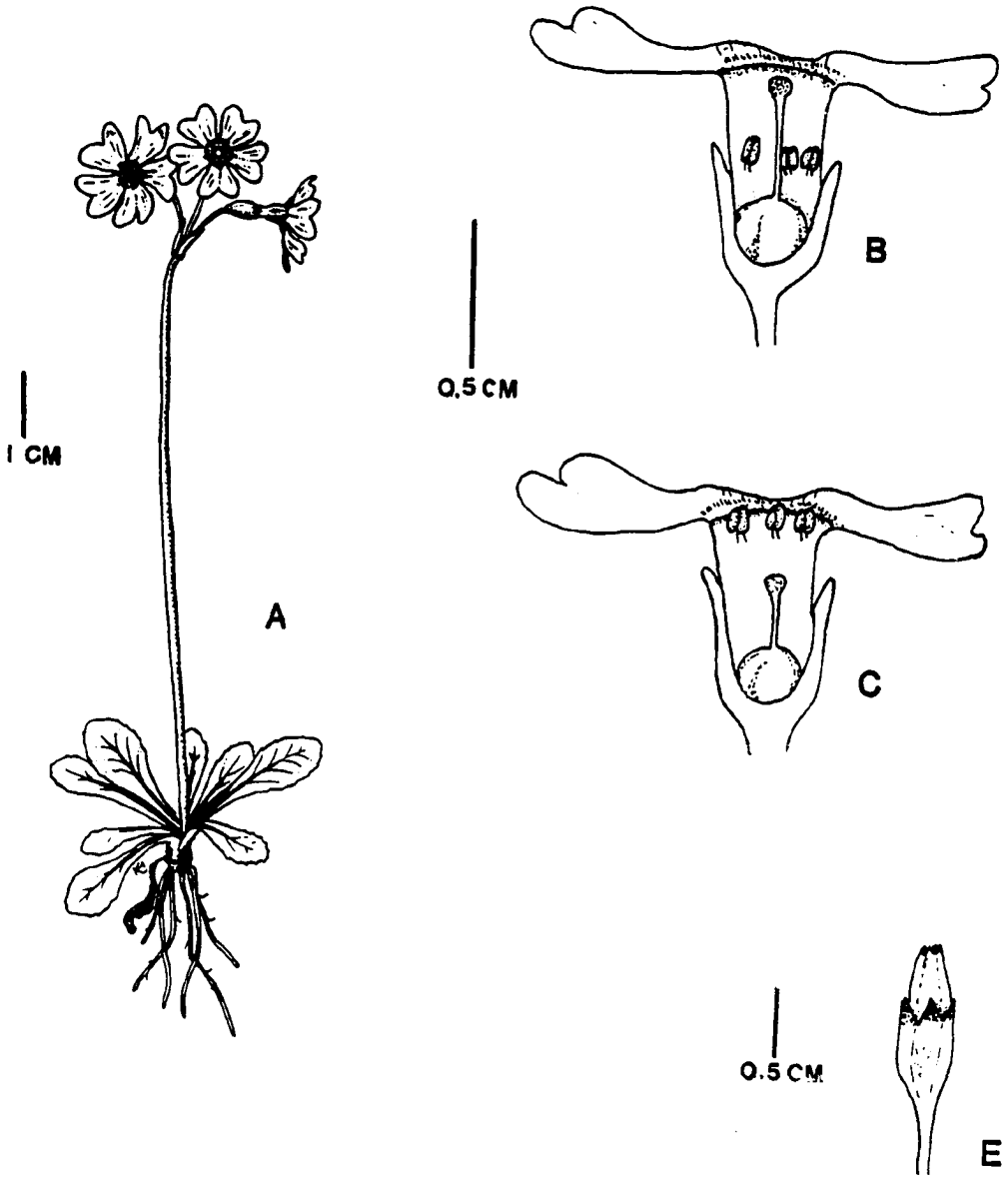


Fig. 2.11. *Primula mistassinica.* A. Habit. B. Pin flower. C. Thrum flower. D. Bracts. E. Capsule.

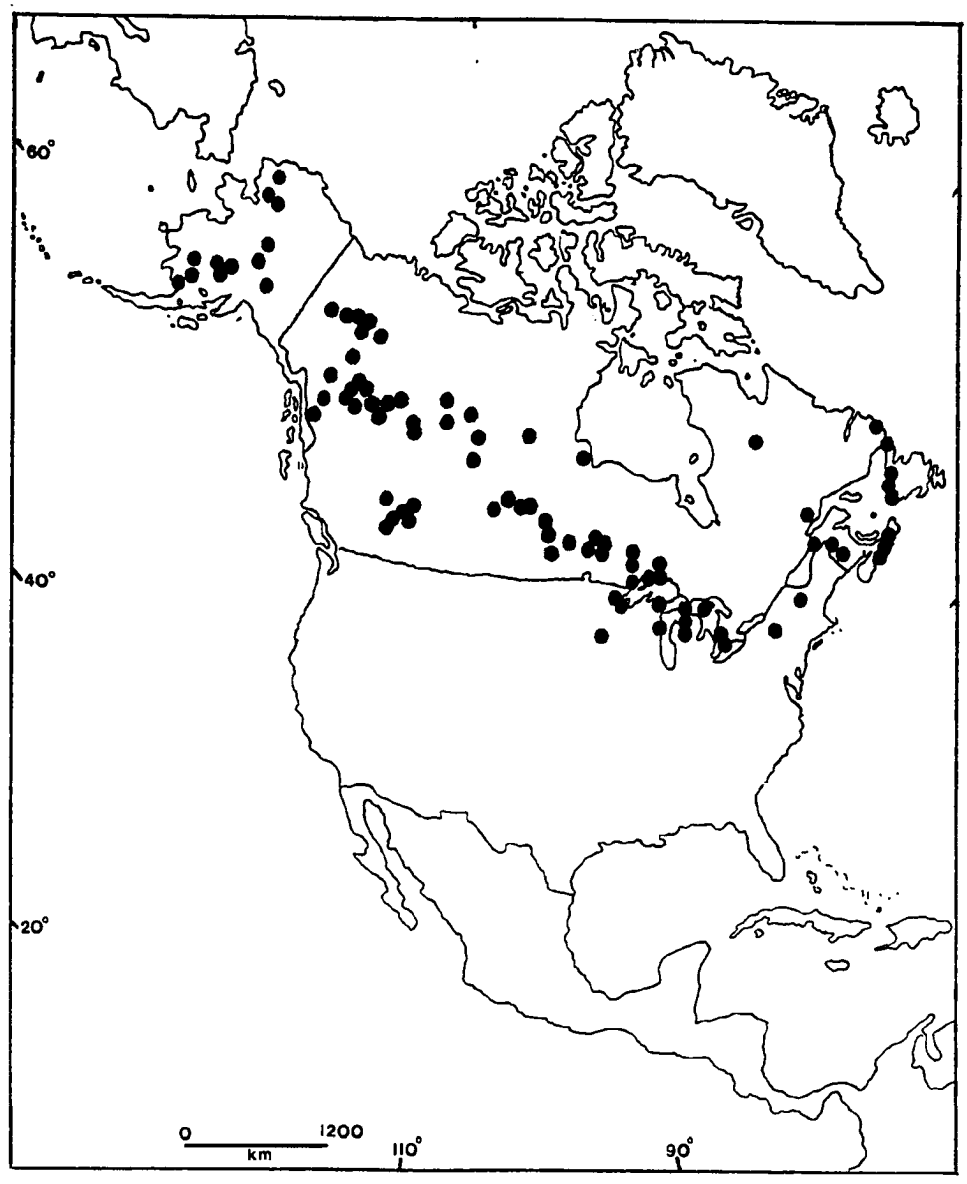


Fig. 2.12. Known range of *Primula mistassinica*.

Primula specuicola Rydberg (Fig. 2.13)

Primula specuicola Rydberg, Studies on the Rocky Mt. Flora XXIX. Bull. Torrey Bot. Club 40: 461-462. 1913. TYPE: UNITED STATES. UTAH. San Juan River, near Bluffs. (Holotype: *Rydberg 9882*. NY!)

Primula hunnewellii Fernald, Rhodora 36:117. 1934. TYPE: UNITED STATES. ARIZONA. Coconino County, north rim of the Grand Canyon. (Holotype: *Hunnewell 10883* in Hunnewell Herbarium. Isotype: GH!)

DESCRIPTION

Plants heavily farinose. Scape to 25 cm tall. Leaves spathulate, including petioles to 13 cm long, blade to 2 cm wide, margins strongly sinuate-dentate, blade gradually narrowing to a broadly winged petiole. Involucral bracts lanceolate, plane at base and involute above, 0.5-1 cm long. Umbels loose, (6)10-25 flowered, pedicels ascending, 1-3 cm long. Flowers distylous. Calyx green, campanulate, obscurely ribbed, 0.3-0.5 cm long, divided to 1/3 its length by lanceolate teeth covered with capitate glands. Corolla dark violet, with a yellow throat; limb 1-1.6 cm broad, tube 0.8-1 cm long, twice the length of the calyx. Anthers ca 1.5 mm long, stamens located in the middle of the corolla tube in pin plants. Stigma capitate, located in upper 1/3 of corolla tube in pin plants, positions of anthers and stigma reciprocal in thrum plants. Pollen dimorphic, ca 10 μm diam. in pin plants, ca 12 μm diam. in thrum plants. Capsule elliptical, slightly shorter than the calyx. Seeds ca 0.5 mm long, reticulate. Chromosome number: $2n = 18$ (Vogelmann 1960).

Habitat: In canyons on limestone cliff faces with moist seepage areas.

Range: southern Utah and northern Arizona (Fig. 2.14).

Representative specimens examined.

ARIZONA. Coconino Co., Colorado River 40.75 miles below Lee's Ferry: *Holmgren et al. 29 Apr 1970* (COLO); Grand Canyon: *Hunnewell 10883* . UTAH.

Bluff: *Gooding 31 Mar 1940* (GH), *Holmgren 3175* (NY), *3185* (GH, NY), *Maguire et al. 5123, 5122* (GH), *Ripley and Barneby 5366* (NY); Cottonwood Wash: *Eastwood 68* (GH), *Holmgren 3190* (COLO, GH, NY), *Scorup in Feb 1912* (GH); Coyote Canyon: *Welsh and Neese 20989, 20996* (NY). Canyonlands National Park, Green River: *Welsh 8822* (COLO); Dark Canyon: *Shultz and Shultz 2002, Shultz and Shultz 2100* (COLO); Glen Canyon, Hole in the Rock: *Karron 102* (NY); Lake Powell: *Welsh 22859, Welsh et al. 2200* (NY); Marble Canyon: *Holmgren et al. 15577* (NY) Moab: *Jones 7 Jun 1913* (GH, NY), *Shultz and Shultz 2135* (COLO); Schafer Canyon, near Dead Horse Point: *Holmgren and Tippets 12852* (NY).

DISCUSSION

Primula specuicola is a distinctive species with large, deep violet corollas, long pedicels, and large, sharply dentate, farinose leaves. A few specimens with short pedicels can approach the habit of *P. incana* but this species is readily distinguished by its smaller, homostylous flowers and longer capsules as well as by its higher chromosome number.

A specimen from the Grand Canyon with a more exserted capsule than the type material from Utah was given the name *P. hunnewellii* by Fernald (1934). The Arizona plants resemble the type material of *P. specuicola* in all other aspects of morphology, cytology, and ecology, and Vogelmann (1960) has placed the name *P. hunnewellii* under *P. specuicola.*

Primula specuicola is an endemic of the canyon country of southern Utah and northern Arizona. While it has not yet been reported from Colorado, similar habitat can be found in the southwestern part of that state, and the species is likely to grow there as well.

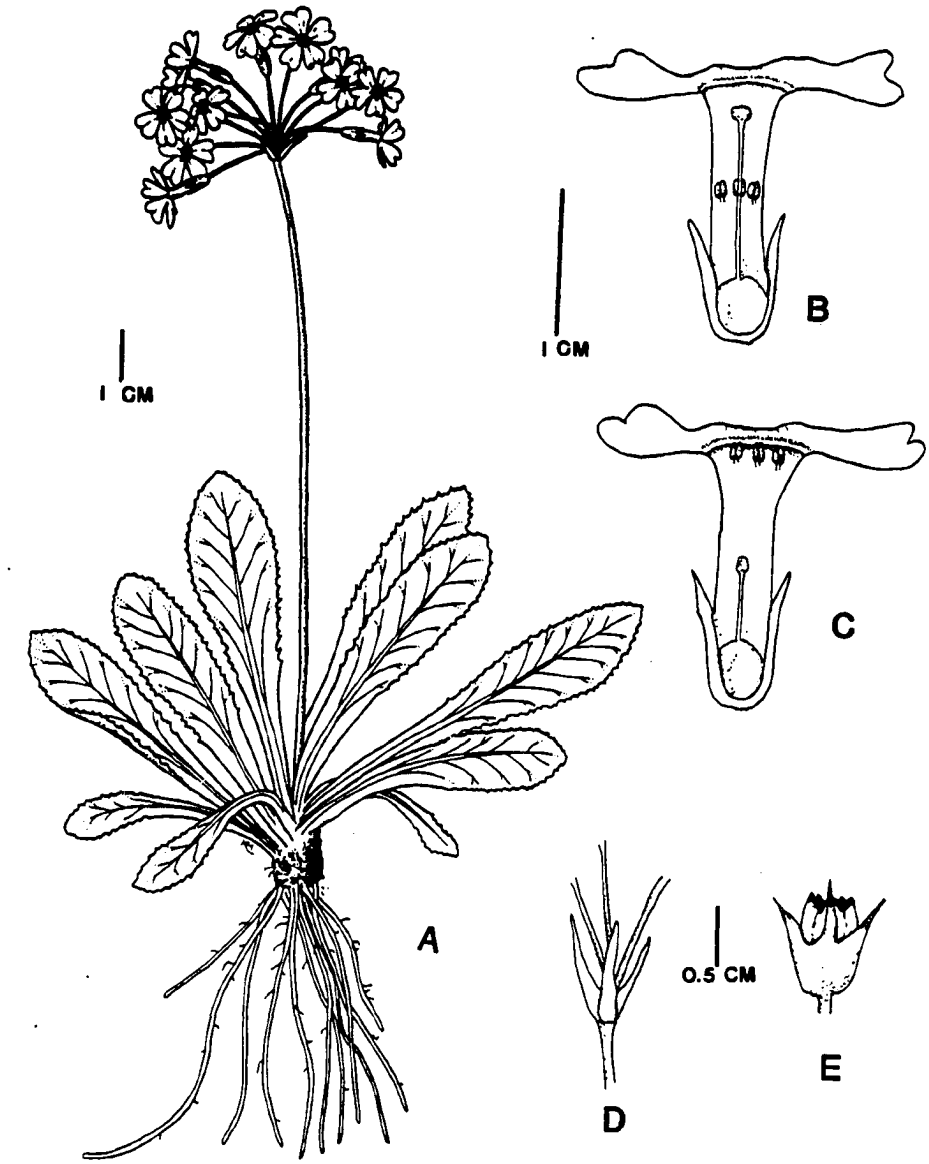


Fig. 2.13. *Primula specuicola.* A. Habit. B. Pin flower. C. Thrum flower. D. Bracts. E. Capsule.

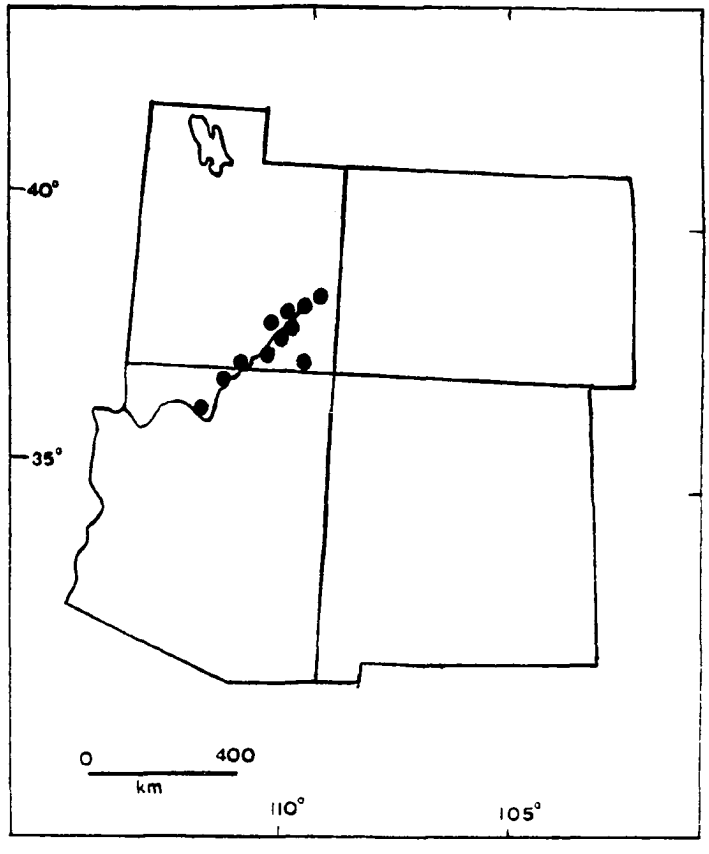


Fig. 2.14. Known range of *Primula specuicola*.

Primula stricta Hornemann (Fig. 2.15)

Primula stricta Hornemann *in* Oeder, Flora Danicae 8(24), t. 1385. 1810. *P. hornemanniana* Lehm. Monogr. Gen. Prim. 55. 1817. TYPE: Norway: Tolgen and Roraas. *Hornemann s.n.* (Holotype: C, microfiche ALA!) *P. farinosa* var. *groenlandica* Pax in Engler, Pflanzenr. Primulaceae 84. 1905.-pro parte .

DESCRIPTION

Plants efarinose or sparingly farinose. Scape 8-15 (18.5) cm tall. Leaves including petiole 1-6 cm long, oblanceolate to spathulate, margins slightly denticulate to almost entire, blade 0.3 to 1.1 cm broad, gradually narrowing onto winged petioles. Involucral bracts lanceolate, acute at the tip, saccate at base, involute above, 0.6 to 1.0 cm long. Umbel 2-9 flowered, pedicels 0.1-0.8 cm long, elongating slightly in fruit. Flowers homostylous. Calyx green or with purple striations, campanulate, obscurely ribbed, 0.4 to 0.6 cm long, divided up to 1/3 by lanceolate teeth, with capitate glands on the margins, somewhat white farinose on the inner surface. Corolla tube 0.4 to 0.7 cm long, slightly exserted from calyx at anthesis, limb 0.5 to 0.8 cm wide, lobes slightly emarginate. Stigmas capitate, located just below the annulus. Stamens ca 0.75 mm long, anthers adjacent to stigma. Pollen ca. 19 µm diam., exine reticulate, 5-syncolpate. Capsules ovoid-elliptical, slightly longer than the calyx. Seeds strongly reticulate, ca 0.3 mm long. Chromosome number: $2n$ = 126 (unknown location: Bruun 1930; Iceland: Löve and Löve 1956; Manitoba: Löve and Ritchie 1966). $2n > 90$ (Norway: Laane 1967).

Habitat: Coastal regions including marshes, stable dunes and beach ridges, more rare inland along rivers; associated species in the Hudson Bay region: *Carex microglochin* Wahlenb., *Carex saxatilis* L., *Festuca rubra* L., *Luzula sudetica* (Willd.) DC, *Parnassia palustris* L., *Primula egaliksensis* Wormskj., and *Rhinanthus cristo-galli* (Polunin 1948; Porsild 1955; Ritchie 1956; Riley and McKay 1980).

Range: In North America throughout the southern islands of the Canadian Arctic

Archipelago and Hudson Bay region, east through Greenland and Scandinavia to Novaya Zemlia (Fig. 2.16)

Representative specimens examined.

CANADA. LABRADOR. Cape Mugford: *Porsild 206* (GH); Kangalaksiorvik: *Abbé 501* (E, K); Nain: *Lundberg s.n.* (BM); Turnavik: *Porsild 109* (US); Ungava Bay: *Bonde et al. 48199* (COLO), *Rousseau and Rousseau 1159, 1160* (DAO), *Rousseau 1160* (BM). MANITOBA. Churchill: *Beckett 260* (BM), *3353* (CAN), *Blagan 24 Jun 1965* (ISC), *Bryant in Jun 1930* (CAN), *Cairns 89722* (CAN), *Gardner 70* (CAN); *Gillett 2575* (COLO), *Hyde 171* (CAN), *Lamoureux 1696* (CAN), *Macoun 79, 388* (E, K), *Marris 10469, 10533* (BM), *Polunin 49* (E), *Porsild 18616* (CAN), *5492A* (BM, CAN, US), *Rossbach 7060* (CAN), *Schofield and Crum 6514* (CAN), *Scoggan 187* (CAN), *Swales 3 Jul 1963* (UBC); Gillam: *Marris 10575, 10585* (BM), *Schofield 1367* (BM); Warkworth Creek: *Howe 170, 98* (CAN). NORTHWEST TERRITORIES. Anderson River: *Scotter 7294* (DAO); Bathurst Inlet: *Blake Aug 1962* (CAN), *Kelsall and McEwan 49, 139* (CAN), *Scotter and Zoltai 31868* (DAO); Belcher Islands: *Abbé et al. 3998* (DAO), *Bursa 23* (COLO), *Edmonds in Aug 1978* (DAO); Blachford Lake: *Scotter 1027* (DAO); Bernard Harbor: *Johansen 347* (CAN, US); Burnside Harbor: *Oldenburg 44-820* (UBC); Cairn Island: *Abbé and Abbé 3012* (COLO), *Abbé and Abbé 3100* (CAS); Cape Parry Peninsula: *Scotter and Zoltai 25617A* (DAO); Coronation Gulf: *Cox and O'Neil 581* (BM, CAN); Eskimo Harbor: *Williams 40* (CAN); Gilmore Island: *Manning 21 August 1971* (DAO); Gordon Lake: *Henderson 23* (CAN), *Host s.n.* (DAO 178503); Great Bear Lake: *Porsild and Porsild 5180* (CAN); Hudson Strait: *Polunin 1516* (E); Kugong Island: *Manning 19 Jun 1971, 21 Jun 1971* (DAO); Kidney Island: *Manning 6 August 1971* (DAO); Mistake Bay: *Porsild 5710, 5711, 5712* (CAN); Rankin Inlet: *Gillett 16038, 16044* (CAN); Read Island: *Oldenburg 43-962* (GH), *Ross 26A* (GH); Thelon River: *Kuyt 68* (CAN), *Rossback 6516* (CAN); Tsichu: *Hopp 26 Jun 1960* (CAN). NEWFOUNDLAND. Belle Isle: *Wiegand and Hotchkiss 28904* (ISC). QUEBEC. Cape Jones: *Abbé and Marr 4115* (BM, DAO), *Dutilly et al. 32652*

(DAO); Cape Smith: *Polunin 1304* (E); Great Whale River: *Savile 182, 183 , 237, 306, 396* (DAO); Hudson Bay Islands, Richmond Gulf: *Abbé and Abbé 3012* (DAO), *Abbé and Abbé 3240* (BM, US), *Abbé and Abbé 3302* (BM), *Abbé et al. 3100* (BM, US), *Abbé et al. 3240* (BM, CAS, COLO), *Abbé et al. 3302, 3892* (CAS).

GREENLAND. Ikerasaki Umaneq District: *Porsild and Porsild 4 Jul 1929* (GH); Kugsinerssuaq: *Porsild 11 Jul 1923* (GH), *Porsild and Porsild 4 Jul 1929* (GH); Itivdleq Fjord: *Posild 6 Jul 1926* (GH); Qeqertat: *Porsild and Porsild on 11 July 1929* (US); Rypefjord: *Holmen and Laegaard 61* (ALA, COLO, DAO); Scoresby Sund: *Marris 994, 1544, 1547, 2019* (BM), *Halliday 118/71* (ALA, E); Sondre Strømfjord: *Böcher 556* (DAO), Holt 637 (BM, COLO, DAO, E); Strindberg Halvo: *Seiden 365* (CAS).

NORWAY. Dovre: *Ahlberg Jul 1875* (NY), *Johanson Jul 1984* (NY), *Schlyter 2039* (CAS); Sor-Trondelag: *Fondal 7 Jul 1957* (ALA); Trøms Fylke: *Alava et al. 4400* (ALA).

SWEDEN. Abiskjokk: *Moldenke and Moldenke 20838* (NY); Jamtland: *Lange 1282* (ALA, COLO, K); Ostersund: *Solberg 14 Jun 1861* (NY); Torn Lappmark: *Alm 2241* (CAS), *Selander 5 Jul 1905* (GH); Wikstroem: *Londer 1856* (NY).

USSR. NOVAYA ZEMLIA. Karmakulski: *Ekstrom 26 Aug 1901* (GH, NY).

DISCUSSION

In its most typical form, *P. stricta* is a short plant with tightly capitate umbels, small emarginate corollas, and ovoid capsules barely longer than the calyx. While variable in height and in number of flowers, the morphology of the species remains generally consistent across the range in the Canadian and European Arctic. This consistency in *P. stricta*, however, has been obscured in Europe by confusion with a form of *P. egaliksensis* and in northwestern North America with *P. incana*.

The misapplication of the name *P. stricta* var. *groenlandica* Warming was discussed in detail by Fernald (1928) who conclusively showed that the lavender-flowered taxon named by Warming was not a variant of *P stricta*, but rather a color morph of *P. egaliksensis*, which until then was believed to have only white

flowers. Fernald renamed *P. stricta* var. *groenlandica* as *P. egaliksensis* f.*violacea*, and this nomenclature has since been in general use (Smith and Fletcher 1943; Polunin 1959; Hultén 1968; Scoggan 1979).

Primula stricta is most similar to *P. incana* Jones, and some specimens from western and central Canada are almost indistinguishable during certain growth stages. *P. stricta* is less than one third the height of *P. incana*, it lacks the dense farina of the latter species except on the inner surface of the calyx, and it has involute rather than flat involucral bracts. *Primula stricta* also has ovoid rather than cylindrical capsules, and they barely exceed the calyx whereas the capsules of *P. incana* are twice the length of the calyx. These morphological differences between the two species are supported by cytological differences: *P. stricta* is a 14-ploid ($2n = 126$) and *P. incana* is a hexaploid ($2n = 54$).

In western North America, *P. stricta* has been erroneously reported in the Yukon Territory and Alaska (Hultén 1968; Porsild 1966, Scoggan 1979). Most of the records west of the MacKenzie Basin are based on misidentified specimens of *P. incana*. The confusion of the two taxa here is understandable, since in the interior of the Yukon, particularly in the saline clay pans around Kluane Lake, *P. incana* takes a small efarinose form with depauperate umbels that is very similar to *P. stricta*. Although this ecotype superficially resembles the high arctic species in size and habit, it shows the distinctive bracts and capsules of *P. incana*. Furthermore, when transplanted to gardens in Fairbanks, the dwarf plants regained the tall farinose appearance that is typical of *P. incana*. Chromosome counts have confirmed that the Yukon populations are *P. incana* and not *P. stricta* (*Kelso and Holmes 84-37* at ALA, $2n = 54$)

In Alaska, Hultén (1968) reported *P. stricta* in the interior, on the Seward Peninsula and on the arctic seacoast. These records are also based on misidentifications. On the Seward Peninsula the specimens used for the records (Hultén 1948) are *P. anvilensis* (e.g. *Hutchinson 313-318, 313-331* E! K!); on the arctic coast they are *P. borealis* (e.g. *Johansen 265* CAN!), and in the interior of Alaska, they are *P. incana* (Copper Center: *Heideman 46* US!). The specimens of *P. stricta* cited from the Yukon (Five Finger Rapids: *Tarleton 78;* Lewes River: *Gorman 1052*, both at US!) are also *P. incana*.

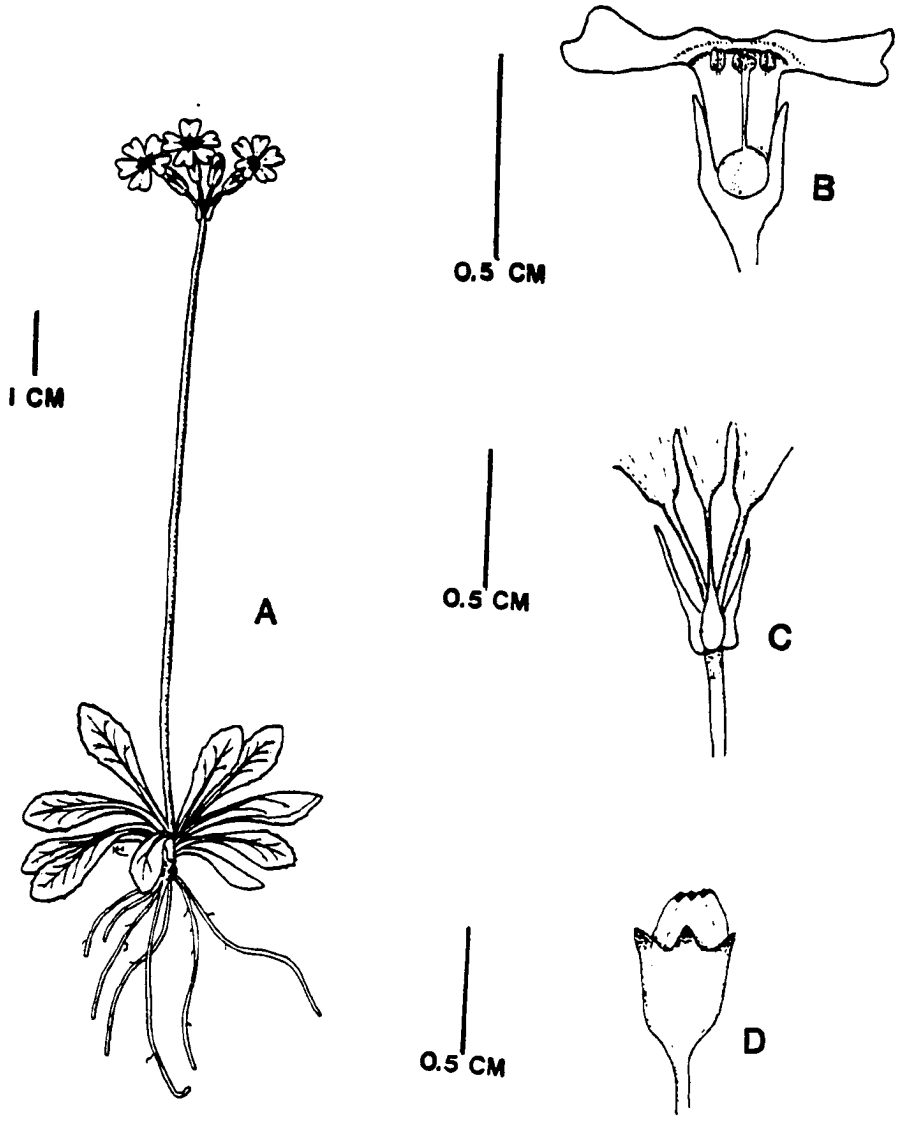


Fig. 2.15. *Primula stricta*. A. Habit. B. Flower. C. Bracts. D. Capsule.

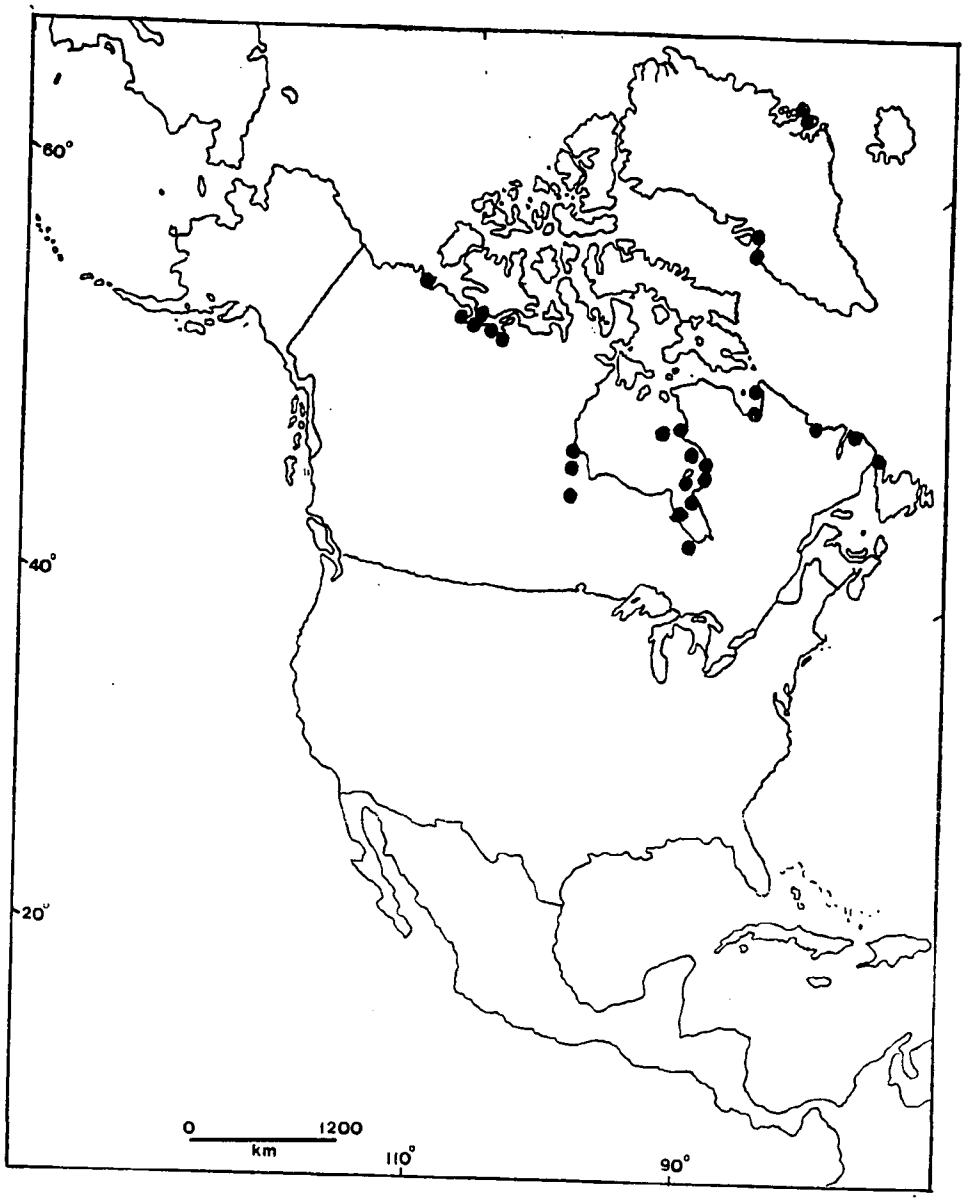


Fig. 2.16. Known range of *Primula stricta* in North America.

Primula section **Armerina** Lindley, Edward's Bot. Reg. 32: t. 31. 1846. TYPE SPECIES: *P. involucrate* Wallich. Plants efarinose, but with jointed hairs. Leaves with revolute vernation, distinctly petiolate on slender elongate petioles; blades entire or slightly undulate. Involucral bracts saccate and usually conspicuosly auriculate at base; pedicels flexuous. Chromosome base number: $x = 11$.
Distribution: Cosmopolitan, north temperate latitudes.
North American representatives:

P. egaliksensis Wormskj. (NE Asia, Alaska-Newfoundland, south to Colorado)
P. nutans Georgi (Europe, Central Asia, NE Asia, Alaska, Yukon)

Schwarz (1968) divided section *Armerina* into two subsections: subsection *Armerina* (including *P. nutans*) and subsection *Chamaecome* (including *P. egaliksensis*). He distinguished the latter section by its persistent rhizomes, in contrast to subsection *Armerina* with rhizomes lasting only a single growing season. At best this distinction seems weak, and at least in Alaska, it is completely false. Consequently, I do not follow the subsectional divisions of Schwarz, and until further studies are possible, treat all the species related to *P. nutans* as members of a single section.

Primula egaliksensis Wormskjold (Fig. 2.17)

Primula egaliksensis Hornemann, in Oeder, *Fl. Danicae* 9: 2. t. 1511. 1816. *P. egaliccensis* Lehm. Monogr. Gen. Prim. 64, t. 8. 1817. TYPE: GREENLAND. Igaliko: *Wormskjiold in 1813* (Holotype: C; Isotype: E!).

P. stricta var. *groenlandica* Warm., Kongl. Svenska Vetenskapsakad. Handl. 12:21. 1887. *P. farinosa* var. *groenlandica* Pax, in Engler, *Das Pflanzenreich,* Primulaceae 84. 1905, pro parte. *P. groenlandica* (Warming) Balfour, J. Royal Hort. Society 34: 182. 1913. *P. egaliksensis* f. *violacea* Fern. Rhodora 30:98. 1928. TYPE: Greenland: Itivnek, Holsteinborg District. *Warming & Holm 13 Jul 1884* (Holotype: C, isotypes: GH! K!).

P. sibirica Hooker, Fl. Bor. Am. 2: 121. 1838, pro parte. *P. sibirica* var. *minor* Duby, in DeCandolle, *Prodromus* 8: 43. 1844.

DESCRIPTION

Plants slender, completely efarinose. Scape 4-12.5 cm tall. Leaves distinctly pedicellate, including the petiole 1.5-5.5 cm long, blade elliptical, to 0.9 cm wide, 0.7-2.5 cm long, margins entire, obscurely undulate or slightly denticulate in age. Involucral bracts lanceolate, to 0.6 cm long, distinctly saccate but not auriculate at the base, somewhat involute above. Umbel 1-3 (6) flowered, pedicels pendant, 0.2-0.9 cm long. Flowers homostylous. Calyx cylindrical, obscurely ribbed, 0.4-0.9 cm long, green or with purple stripes, divided to 1/3 by teeth with glandular cilia on the margins. Corolla white or lavender, throat yellow; limb 0.6-0.8 cm wide, slightly emarginate, tube 0.6-0.8 cm long, equal to or slightly exserted from the calyx. Stamens ca 0.75 mm long, anthers located adjacent to stigmas in upper one third of corolla tube. Stigma cylindrical. Pollen ca 19 µm diam.; exine mesoreticulate, 4-syncolpate. Capsule narrowly cylindrical, twice the length of the calyx. Seeds green to light brown, obscurely reticulate, to 0.5 mm long. Chromosome number $2n = 36$ (Alaska: *Kelso 85-10, Parker 2007,* both at ALA; Colorado: Löve et al. 1971; Greenland: Jørgenson et al. 1958). $2n =$ ca 36 (Alaska: Johnson and Packer 1968). $2n = 40$ (Northeast Siberia: Zhukova et al. 1973; Zhukova 1982). $2n =$ ca 40 (Labrador: Hedburg 1967).

Habitat: In seral herb communities along river and streambanks in damp silt or clay; associated species in Alaska: *Epilobium latifolium* L., *Parnassia palustris* L.; in Colorado growing with *P. incana* Jones; in Hudson Bay region with *P. stricta* Hornem.

Range: Across North America from Alaska to Greenland, known in the south from disjunct locations in South Park, Colorado and northwestern Wyoming; in Asia, known from a few localities on the Chukotsk Peninsula (Fig. 2.18).

Representative specimens examined.

CANADA. ALBERTA. Clearwater Reserve: *Porsild 20670* (CAN); Sunwapta River: *Hermann 12725* (CAN). BRITISH COLUMBIA. Atlin Lake: *Guilliam 10 Jun 1900* (CAN), *Lammers 8* (CAN); Caribou Pass: *Henry 292* (E), *Henry 738* (GH); Graham River: *Henry 330* (E); Haines Road: *Taylor et al. 1307* (CAN, DAO), *Taylor et al. 763* (DAO); Paxton Mt.: *Argus 8969* (CAN). LABRADOR. Anaktalik Bay: *Potter 7724* (GH); Attikamagen Lake: *Harper 3572* (ISC); Duck Island: *Potter and Brierley 3633* (GH); Flowers Cove:*Wallace 72* (GH); Indian Harbor: *Bishop 510* (GH), *Sewall and Weed 10 Jul 1926* (GH), *Abbé and Hogg 503* (GH); Turnavik: *Bishop 511* (E, GH), *Porsild 108* (GH), *Potter 7725* (CAS, GH). MANITOBA. Churchill: *Beckett 261* (BM), *Beckett 3793, 3813* (DAO), *Gillett 1868* (ISC), *1948* (US), *Dore 10068, 1868, 9931, 9939* (DAO), *Polunin 1806* (E), *Porsild 5491* (ALA), *Schofield and Crum 6515* (CAS, COLO); Nelson River: *Schofield 1260* (DAO), *Scoggan 6348* (GH); York Factory: *Scoggan 6095* (GH). NEWFOUNDLAND. Belle Isle: *Fernald et al. 28892* (GH, ISC), *Fernald and Long 28899* (GH), *Fernald and Long 28916* (K), *Gilbert 28893* (ISC), *Long and Gilbert 2889* (GH); Ingornachoix Bay: *Fernald et al. 1952, 1953* (GH); Pistolet Bay: *Fernald and Greene 28917* (GH); St. Barbe: *Fernald et al. 26962* (GH). NORTHWEST TERRITORIES. Baker Lake: *Savile and Watts 1488* (DAO); Belcher Islands: *Bursa 22* (COLO); Burnside Harbor: *Oldenburg 44-820* (UBC); Cairn Island: *Abbé et al. 3099* (COLO); Canol Rd.: *Porsild and Breitung 10314* (GH); Coppermine: *Findlay 118* (BM); Great Bear Lake: *Porsild and Porsild 3235* (GH), *4712A* (BM); Great Slave Lake: *Raup 1229* (GH); Long Island: *Dutilly and*

Lepage 14.194 (DAO); Mackenzie River: *Porsild and Porsild 3391* (GH); McConnell River: *MacInnes 55, 485* (DAO); Chesterfield Inlet: *Savile 1421* (DAO), *Savile and Watts 1455* (DAO), *Savile et al. 1181* (DAO). ONTARIO. Black Duck River: *Moir 1880, 2072* (GH); James Bay, Shipsands Island: *Brunton et al. 410* (DAO); Kapiskau River: *Ringius et al. 856* (DAO); Niskibi River: *Moir 1799* (GH). QUEBEC. Cape Henriette: *Dutilly and Lepage 32147* (DAO); Cape Smith: *Polunin 1302* (E); George River: *Rousseau 1104* (DAO); Great Whale River: *Savile 236, 297* (DAO), *335* (GH), *Abbé and Abbé 3928* (GH); Kogaluk and Payne Rivers: *Rousseau 148* (DAO); Kopaluk Bay: *Rousseau 1080* (DAO, US); Mingan Archipelago: *Marie-Victorin 21830* (DAO); Riviere aux Feuilles: *Legault 6979* (DAO); Rupert House: *Spafford 3* (DAO); Ungava Bay: *MacInnes 5097* (DAO), *Rousseau 213A* (DAO). YUKON. Canol Road: *Porsild and Breitung 10841* (CAN), *10314* (GH); Frances Lake: *Rosie 281* (CAN); Kaskawulsh River: *Pearson 128* (CAN); Lake Atlin: *Wilkinson 6315* (UBC); Lewes River: *Gorman 1059* (CAN); MacKenzie River Basin: *Raup 1230* (ALA); Olgivie Mountains: *Parker 981* (ALA); St. Elias Mts.: *Pearson 67-132A* (CAN).

USA. ALASKA. Alaska Range. Big River: *Drury 4314* (ALA); Big Salmon Fork: *Parker 738* (ALA); Davidson Glacier: *Cooper and Andrews 4 Jul 1929* (ALA); Delta River: *Kelso 85-11* (ALA); Donnelly Creek: *Kelso 85-10, 85-15* (ALA); Dry Creek: *Viereck and Jones 5787* (ALA); Healy: *Anderson 23 Jul 1939* (ISC); Kuskokwim Mts.: *Drury 2594* (GH); Lignite: *Anderson 19 Jul 1931* (ISC). Alexander Archipelago. Glacier Bay: *Hok 6-67, 57-67* (ALA), *Koranda 19 Jun 1962* (DAO); Haines: *Williams 3693* (ALA); Yakutat: *Batten and Murphy 77-87* ALA), *Harms 5224* (ALA), *Walker and Walker 1052* (E, GH). Aleutian Islands. Unalaska: *Evermann 76* (CAS). Brooks Range. Eli River: *Young 4221* (ALA); Kukpowruk River:*Chambers s.n.* (CAS); Last Lake: *Batten and Batten 75-324* (ALA); Lobo Lake: *Batten and Batten 75-598* (ALA); Mt. McGinnis: *Murray 3087* (ALA); Sheenjek River: *Kessel S65* (ALA); Sukakpak Mt.: *Khokhryakov et al. 6510* (ALA), *Murray and Johnson 6267* (ALA); Takahula Lake: *Jorgensen T202* (ALA); Walker Lake: *Smith 2440* (ALA); Wiehl Mt.: *Murray and Johnson 6280* (ALA); Wiseman: *Jordal 1858* (ISC). Chugach Mountains. Copper River Delta: *Parker 2007* (ALA). North Slope. Atkasuq: *Komarkova and Duffy 142* (BM, COLO); *Komarkova et al. 284* (ALA); Arctic Coastal Plain: *Ebersole and Bowman*

228 (COLO); East Oumalik: *Ward 1481* (CAS); Jago River: *LaFlamme in 1984* (ALA); Meade River: *Ward 1124* (CAS). Seward Peninsula. Inmachuk River: *Racine 386* (ALA); Shishmaref: *Rynning 1026* (ALA); Teller: *Scammon 5594* (GH).

DISCUSSION

Primula egaliksensis is a well-marked species easily distinguished by its few-flowered umbels of tiny homostylous flowers and elliptical efarinose leaves . The co-occurrence of lilac and white flowered forms created some initial taxonomic confusion when Warming allied the lilac form in Greenland with *P. stricta* rather than with the white flowered taxon first described by Wormskjold. This confusion was resolved by Fernald (1928) who analyzed both forms in detail and concluded that the violet form was merely a color variant and did not deserve major taxonomic recognition. Fernald noted that both color morphs occur throughout the range of the species, sometimes sympatrically, and he concluded that the white form was an albino condition similar to (albeit more common than) the albino morphs seen in normally violet flowered species such as *P. mistassinica.* My examination of the abundant material now available shows that Fernald was correct in his conclusions. Both white and violet forms are equally common and adjacent populations of the two colors occur. Other than corolla color, there are no morphological differences between the forms. Although *P. egaliksensis* has a wide geographic range, it is never locally abundant. Because of the small flowers and generally short stature, individual plants are inconspicuous even during the brief flowering period.

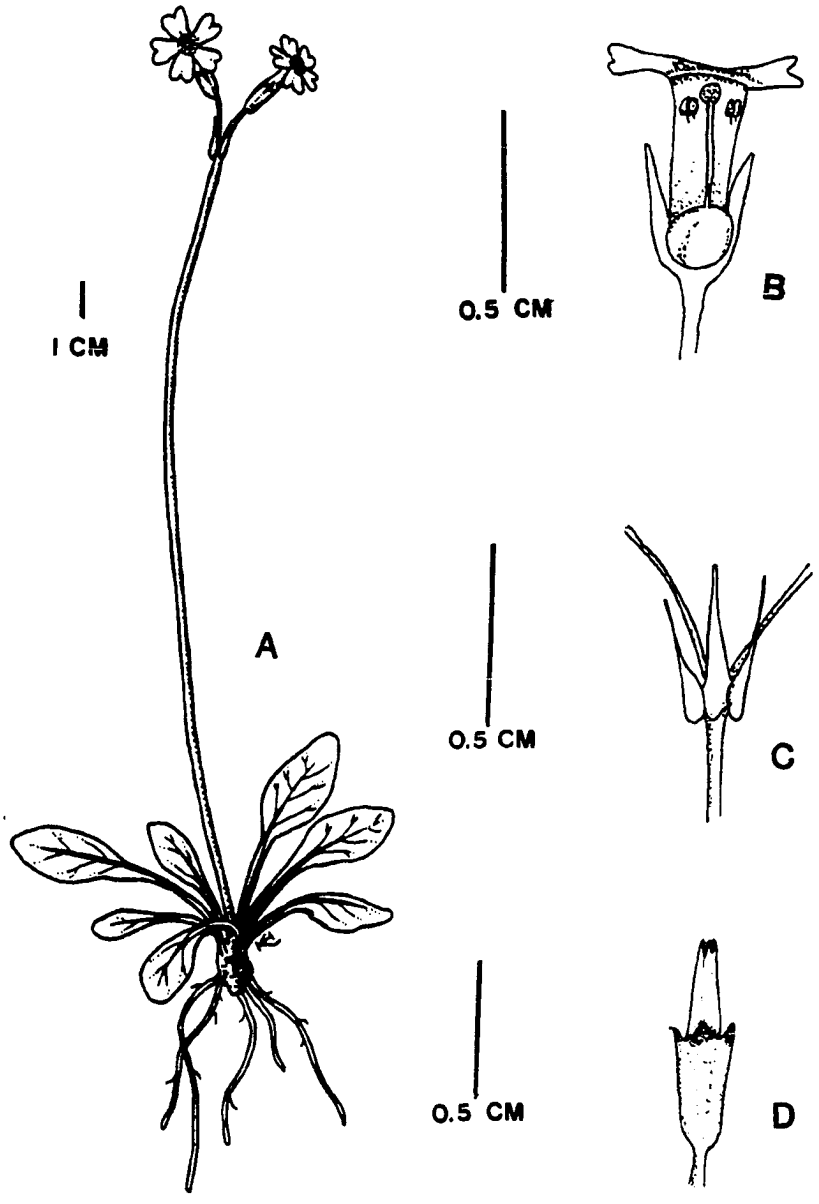


Fig. 2.17. *Primula egaliksensis*. A. Habit. B. Flower. C. Bracts. D. Capsule.

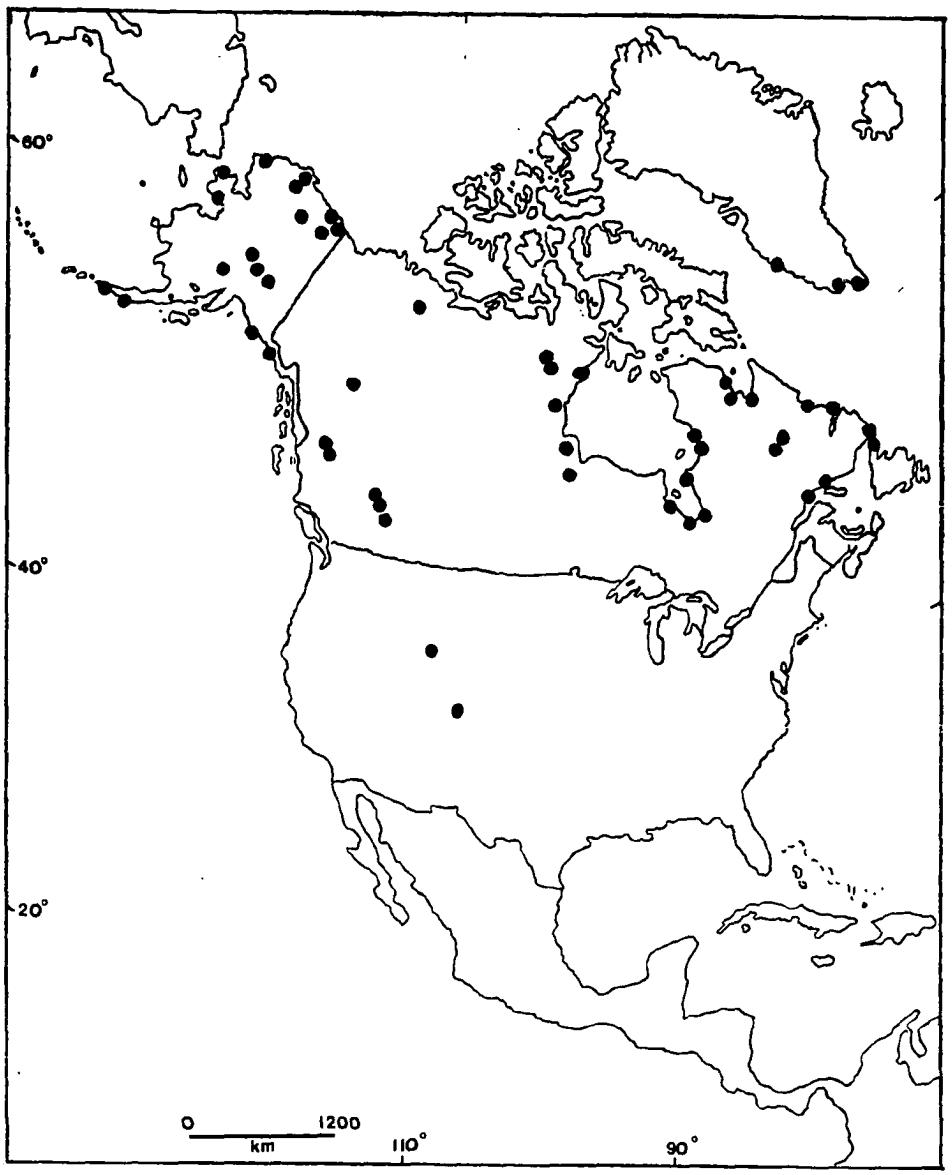


Fig. 2.18. Known range of *Primula egaliksensis* in North America.

Primula nutans Georgi (Fig. 2.19)

Primula nutans Georgi Bemerk. Russ. Reich 1: 200. 1775. *P. sibirica* Jacq. Misc. Austr. 1: 161. 1778. TYPE: *J.G. Gmelin*, Fl. Sib. 4: t. 46. 1769. "Ab Ob fluvio ad transbaicalensis usque ad regiones" (Holotype: LE?).

DESCRIPTION

Plants slender, efarinose, sometimes rhizomatous. Scape 5-20 cm tall. Leaves distinctly pedicellate, including petioles to 3 cm long; blade ovate to slightly elliptical, to 2 cm wide, 1-2 cm long, margins entire. Involucral bracts 0.4-0.6 cm long, oblong, obtuse at the tip, saccate and prominently auriculate at the base. Umbel 2-4 flowered; pedicels nodding, 3 times the length of the bracts. Flowers distylous. Calyx cylindrical, 4-7 mm long, distinctly ribbed, divided to 1/4 its length by obtuse to somewhat acute teeth, with prominent ciliolate glands on the margins. Corolla violet with a yellow throat, tube 0.7-1 cm long, strongly exserted from the calyx in North American specimens; limb 0.9-2 cm wide, lobes cordate. Stamens 1.5-2 mm long, located in middle of corolla tube in pin plants and near top of corolla tube in thrum plants. Stigma cylindrical, located in pin plants slightly above the annulus of corolla tube, and in thrum plants near middle of tube. Pollen dimorphic, ca.16 μm diam. in pin plants, ca 22 μm diam. in thrum plants; exine broadly reticulate, stephanocolpate with 6 obscure furrows. Capsules narrowly cylindrical, twice the length of the calyx. Seeds light brown, ca. 0.5 mm long, rounded, reticulate. Chromosome number: $2n = 22$ (Alaska: *Kelso 84-05* at ALA; Yukon: *Kelso and Holmes 84-21* at ALA; Kamtchatka: Sokolovskaya 1968; Northeast Siberia: Zhukova and Tikhonova 1973; Norway: Engelskon 1979; Borgen and Elven 1983). $2n = 20$ (Mongolia: Hanelt 1973; Lake Baikal, Sibiria: Belaeva and Siplivinsky 1975).

Habitat: In halophytic sedge, grass, and herb meadows: salt marshes and estuaries along the coast, inland in sloughs and river flood plains; associated species in coastal Alaska: *Carex aquatilis* Wahlenb., *Carex subspathacea* Wormskj., *Primula borealis* Duby, *Potentilla egedii* Wormskj.; in interior Alaska: *Carex aquatilis* Wahlenb., *Eriophorum russeolum* E. Fries, *Triglochin palustris* L., *Pedicularis sudetica*

Willd., *Hylocomium spp.*

Range: From Fennoscandia across northern and central Asia, coastal Alaska, rare in the interior of Alaska and the Yukon (Fig. 2.20).

Representative specimens examined.

CANADA. YUKON. Alsek River: *Raup and Raup 11890* (ALA, GH); Bear Creek: *Abbot 18* (DAO), *Raup et al. 13085 , 13931* (GH); Burwash: *Raup et al. 13930* (GH); Donjek River: *Kelso and Holmes 8421* (ALA); Hootalinquah River: *Rude 172* (ISC); Little Braeburn Lake: *Hodgson 29* (DAO); Mackintosh: *Schofield and Crum* (CAS); Pine Creek: *Nowosad 52* (DAO), *Raup and Raup 11747* (GH); Whitehorse/Eagle: *Lohlbrunner 12032* (CAN). USA. ALASKA. Bering Sea Coast, Chevak: *Boise 007* (ALA); Hooper Bay: *Jackson 1099* (ALA); Kashunuk River: *Sherwood 29 Jun 1961* (ALA); Kotlik: *Rouse 44* (ALA, ISC); Mountain Village: *Kyllingstad s.n.* (ISC 309851); Rhodes Wildlife Refuge: *Boise 6-39* (ALA); Unalakleet: *Anderson 3295* (ISC). Brooks Range, Imiaknikpak Lake: *Murray 4284, 4354* (ALA). Chukchi Sea Coast, Cape Beaufort: *Argus and Chunys 5562* (GH); Cape Thompson: *Belson 19 Jul 1960* (ALA); Kotzebue: *Anderson 4755B* (ISC), *Pegau 14-70* (ALA), *Welsh 5723A, 5839* (ISC). Seward Peninsula, Buckland River: *Rynning 995* (ALA); Cape Wooley: *McCaffrey in 1984* (ALA); Elim:*Wilson in 1937* (ISC); Fort Davis, Nome River: *Kelso 83-159, 84-114* (ALA),*Williams 477* (CAS); Golovin: *Anderson 3390* (ISC), *Kaufman in 1984* (ALA); Mountains of the Moon: *Springer in 1970* (ALA); Nome: *Anderson 3231A* (ISC, K), *Becker 57* (ALA); *Hutchinson 296-297* (K), *Kelso 83-99* (ALA); *Lepage 23940* (DAO), *Thornton 2138* (K), *Welsh 5958* (ISC); Safety Lagoon: *Kelso 83-18* (ALA); Teller: *Scammon 5592* (GH); Wooley Lagoon: *Kelso 82-58* (ALA). Tanana Valley. Northway: *Anderson 9226* (ISC),*Williams 549* (ISC), *Kelso and Holmes 84-21* (ALA).

Primula nutans* subsp. *finmarchia (Jacq.) A. Löve and D. Löve

Primula finmarchia Jacq. Misc. Austr. 1:160. 1778. *P. sibirica* Jacq. var. *finmarchia* (Jacq.) Pax, Engler, Pflanzenreich, Primulaceae 77. 1905. *P. sibirica* Jacq. subsp. *finmarchia* (Jacq.) Hultén in Fl. Alaska and Yukon. 1948. *P. nutans* subsp. *finmarchia* (Jacq.) A. Löve and D. Löve, Bot. Not., 114: 54. 1961.

TYPE: Oeder, Fl. Danicae 2: t. 188. 1765. (Holotype: C?)

DESCRIPTION

Differs from subsp. *nutans* only in the shorter corolla tube which is equal in length to the calyx.

Range: Fennoscandia (Fig. 2.20).

DISCUSSION

Until recently, *P. nutans* Georgi has been known as *P. sibirica* Jacq. By the rules of the International Code of Botanical Nomenclature, the name *P. nutans* must be used because it antedates the nomenclature of Jacquin by three years. Both Georgi and Jacquin used as type material the illustration and description of a Siberian plant by Gmelin (1769) who did not name his taxon beyond the genus level. Jacquin apparently was not aware of the treatment of Georgi and applied his own epithet *P. sibirica* to the taxon described and illustrated by Gmelin. This name was used by Duby (1844) in his monograph of the genus and it became codified through that application in a well-known manuscript as the work of Georgi slipped into obscurity. Smith and Fletcher (1943) were aware of the treatment of Georgi and listed *P. nutans* as a synonym of *P. sibirica,* but with a later and erronious date of publication (1797). Since the true date of publication of the name *P. nutans* is 1772, it takes precedence over *P. sibirica,* published in 1775. This nomenclatural change is discussed by Schwarz (1968) and is used in contemporary European literature (Tutin et al. 1972).

The use of the name *P. nutans* for the Eurasiatic taxon described by Georgi poses a nomenclatural conflict with another taxon, *P. nutans* Delavey, from China (section *Soldanelloides*). By the rules of nomenclature, this taxon must become *P. flaccida* Balakr. The nomenclatural shuffling of the two *P. nutans* species is a

problem for horticulturists, since *P. nutans* sensu Delavay is a favorite cultivated *Primula.* In horticultural contexts, the authority is usually not given with the scientific name, and it is frequently difficult to tell which species is meant.

Although *P. nutans* Georgi is geographically widespread, the morphology of the species is remarkably consistent. The only significant variation is in the relative lengths of calyx and corolla tube. Specimens from Fennoscandia have a short corolla tube only slightly longer than the calyx, while in Asiatic and North American specimens the corolla tube is twice the length of the calyx. The Scandinavian morph is now treated as *P. nutans* subsp. *finmarchia* (Löve and Löve 1961, Mäkinen and Mäkinen 1964).

Hultén (1971) discussed the circumpolar distribution of *P. nutans.* In mountainous regions of central Asia, Federov (1952) recognized three closely related taxa: *P. iljinski* Fed., *P. knorringiana* Fed., and *P. pamirica* Fed., but these were seen as only dubiously distinct by Hultén (1971).

In western Alaska *P. nutans* is commonly found in estuarine marshes. It can be sympatric with *P. borealis* Duby and the two species are often found mixed on herbarium sheets. *P. nutans* is easily distinguished from *P. borealis* by its ovate pedicellate leaves and auriculate bracts. It blooms about two weeks later than *P. borealis,* and unlike *P. borealis,* prefers continually saturated soil.

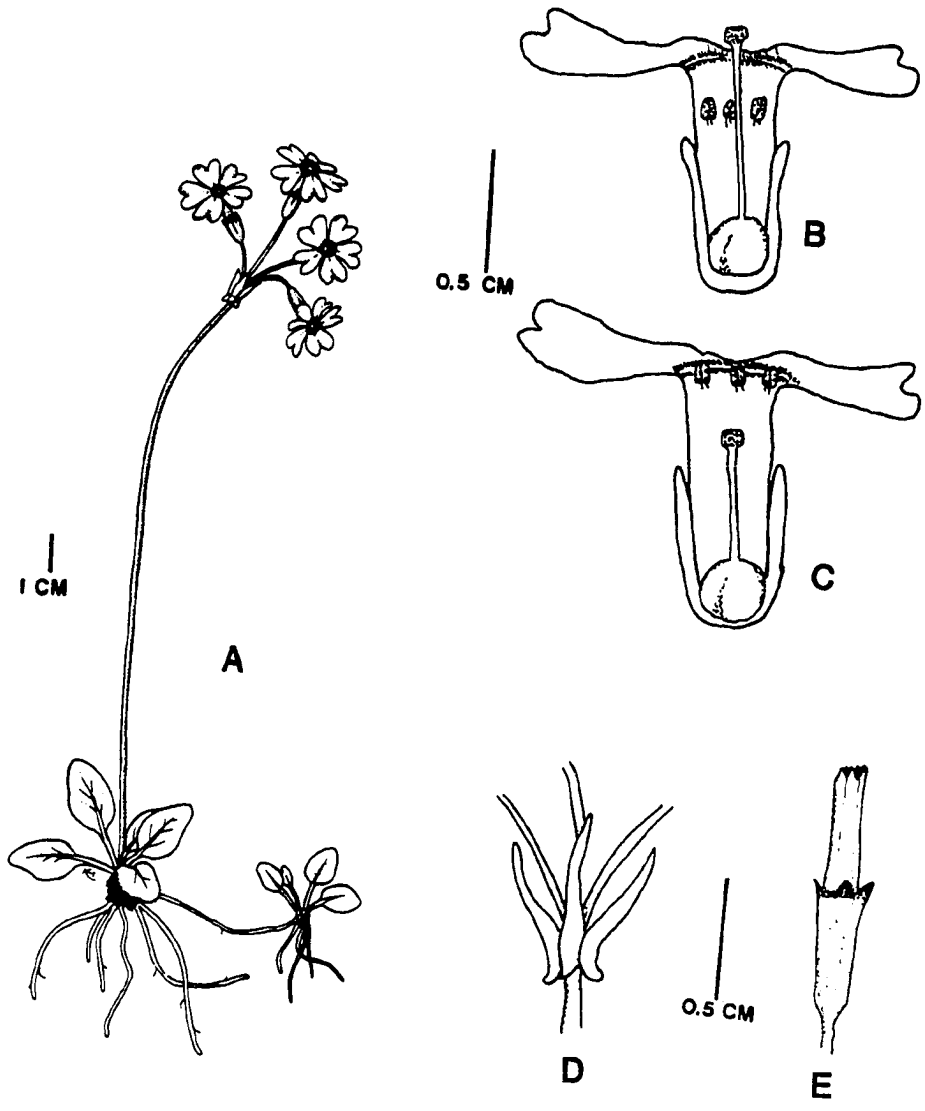


Fig. 2.19. *Primula nutans*. A. Habit. B. Pin flower. C. Thrum flower. D. Bracts. E. Capsule.

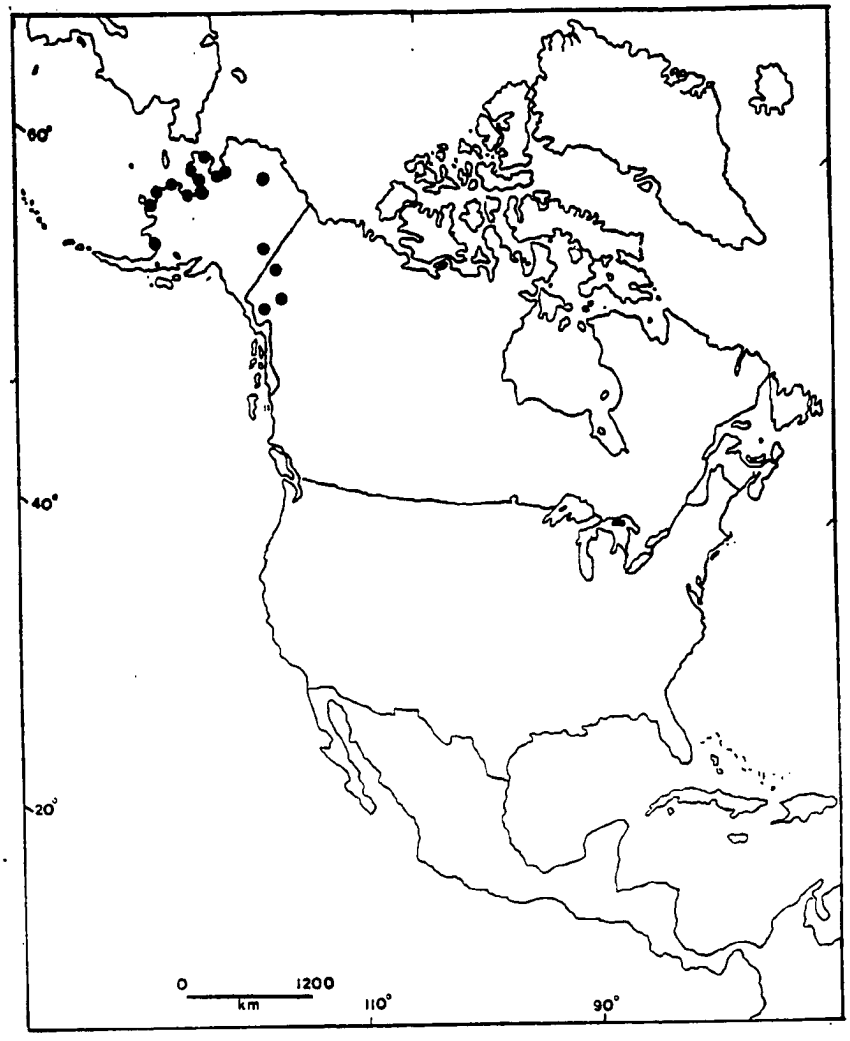


Fig. 2.20. Known range of *Primula nutans* in North America.

Primula section **Crystallophlomis** Rupr., Bull. Acad. Imp. Sci. St. Petersberg. 6: 218. TYPE SPECIES: *P. nivalis* Pallas. Plants with farinose basal bud scales. Leaves with revolute vernation and imbricate sheathlike petioles; blades lanceolate or oblanceolate, fleshy or membranaceous, glabrous, venation obscure. Inflorescence a simple umbel subtended by involucral bracts never saccate at base. Flowers magenta, yellow or white, corolla lobes entire or only slightly emarginate.
Chromosome base number: $x = 11$.
Distribution: Caucasus, Central Asia, Himalayas, China, NE Asia, Alaska.
North American representatives:

P. eximia Greene (NE Asia, Alaska)

P. tschuktschorum (NE Asia, Alaska)

Primula tschuktschorum Kjellman (Fig. 2.21)

Primula tschuktschorum Kjellman, Vega Expeditionens Vetenskapliga Iakttagelser 1: 516, t. 9. 1882. *P. pumila* (Ledeb.) Pax, Bot. Jahrb., 10: 208. 1889. TYPE: U.S.S.R. CHUKOTSK PENINSULA: St. Lawrence Bay, 20-21 Jun 1879, *Kjellman s.n.* (Holotype: S!).

P. pumila var. *ledebouriana* Busch, Fl. Sib. et Orient. Extrem. 4: 75. 1925, pro parte.

P. tschuktschorum subsp. *tschuktschorum* var. *beringensis* A. E. Porsild, Canad. Field Naturalist 79: 87. 1965. *P. tschuktschorum* subsp. *beringensis* (A.E. Porsild) Yurtsev & Kozhevnikov, Bot. Zhurn. 57: 73. 1973. *P. beringensis* (A. E. Porsild) Yurtsev, Bot. Zhurn. 60: 242. 1975. TYPE: UNITED STATES. ALASKA: St. Lawrence Island, Boxer Bay, in 1960, *Sauer s.n.* (Holotype: CAN!; Isotype: WIS).

DESCRIPTION

Plants completely efarinose, glabrous. Scapes to 10 cm tall. Leaves to 4 cm long, less than 0.4 cm wide, linear-lanceolate, entire or remotely dentate at the apex; petioles obsolete. Involucral bracts lanceolate, to 1 cm long, acute or obtuse at tip, flat at the base. Umbel 1-3 flowered; pedicels 0.2-1 cm long. Flowers distylous. Calyx green or greenish-black, 0.5-0.7 cm long, deeply divided by narrow teeth. Corolla rose-magenta, the tube equal in length to the calyx; limb to 1.2 cm diam.; lobes usually entire, sometimes cleft to the base. Stamens ca 1 mm long, anthers 0.3-0.5 cm below the throat of the corolla in pin plants. Stigma capitate, in pin plants located near throat of corolla tube, in thrum plants positions reciprocal. Pollen ca 17 μm diam. in pin plants, ca 22 μm diam. in thrum plants; exine reticulate, 3-syncolpate. Capsule cylindrical at maturity, twice the length of the calyx. Seeds 1-2 mm long, medium brown, vesiculate. Chromosome number: $2n = 22$ (Cape Prince of Wales, Alaska: *Kelso 83-103* at ALA; Chukotsk Peninsula, Siberia: Zhukova 1982).

Habitat: Frost boils in herb-sedge communities and in gravel along small streams where soil is saturated during most of the growing season; from sea level to alpine elevations; associated species: *Carex aquatilis* Wahlenb., *Juncus biglumis* L.,

Pedicularis pennellii Hult., *Sagina intermedia* Fenzl, *Salix arctica* Pall.

Range: known only from the Bering Strait area, including St. Lawrence Island, the Chukotsk Peninsula in Siberia and the Seward Peninsula in Alaska (Fig. 2.22).

Representative specimens examined.

UNITED STATES. ALASKA. Seward Peninsula. Mt. Bendeleben: *Kaufman 15 Jul 1984* (ALA); Cape Prince of Wales: *Kelso 81-183, 83-103, 83-290* (ALA), *Kelso et al. 183* (ALA, COLO); Homestake Creek: *Walker 4 Jun 1970* (ALA); Kigluaik Mountains: *Kaufman 6 Jul 1984* (ALA), *Kelso 82-74* (ALA); Kuzitrin Lake: *Racine 310* (ALA). St. Lawrence Island: *Haley s.n.* (CAS), *Young 610* (GH).

DISCUSSION

See *Primula eximia* Greene.

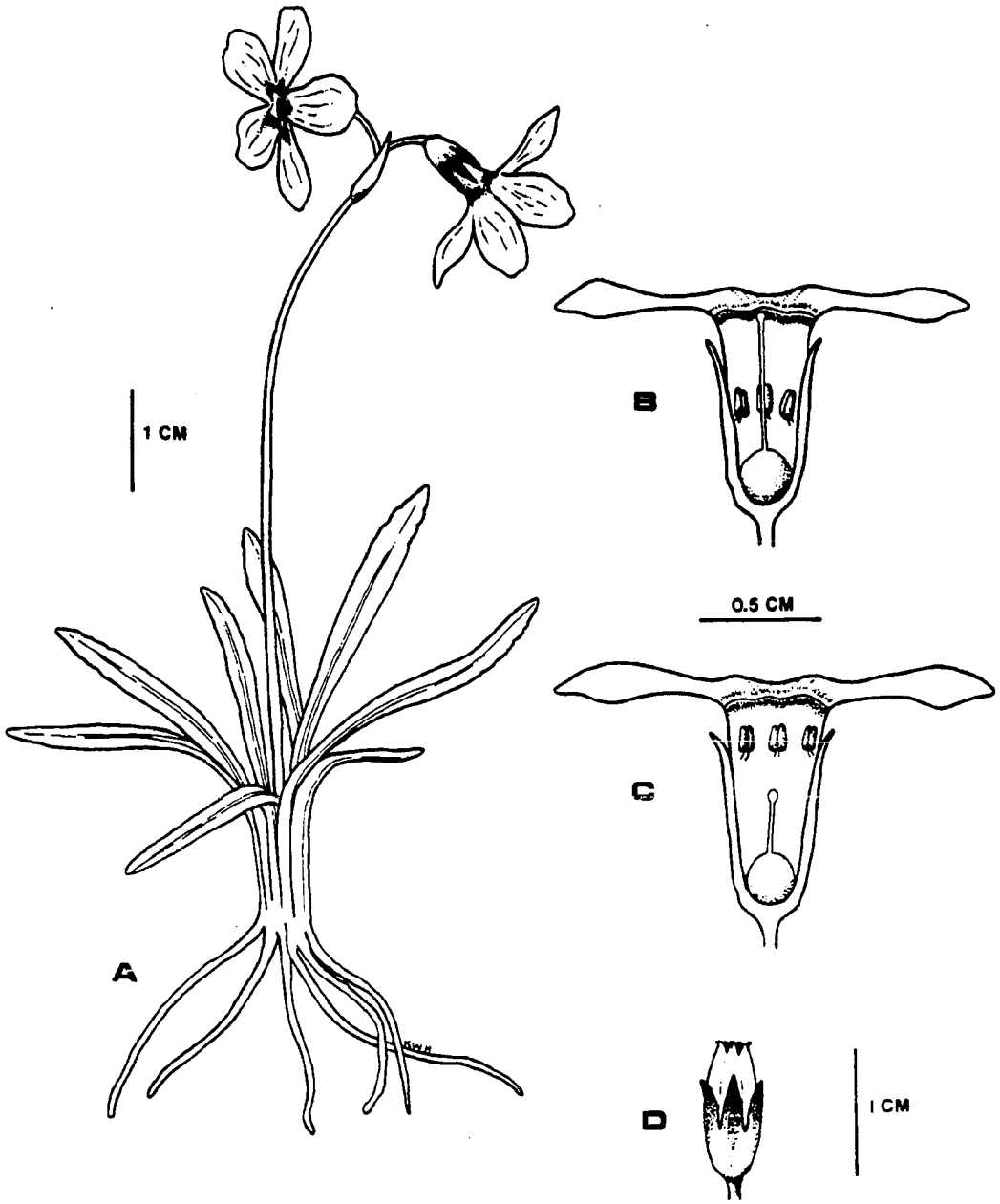


Fig. 2.21. *Primula tschuktschorum*. A. Habit. B. Pin flower. C. Thrum flower. D. Capsule.

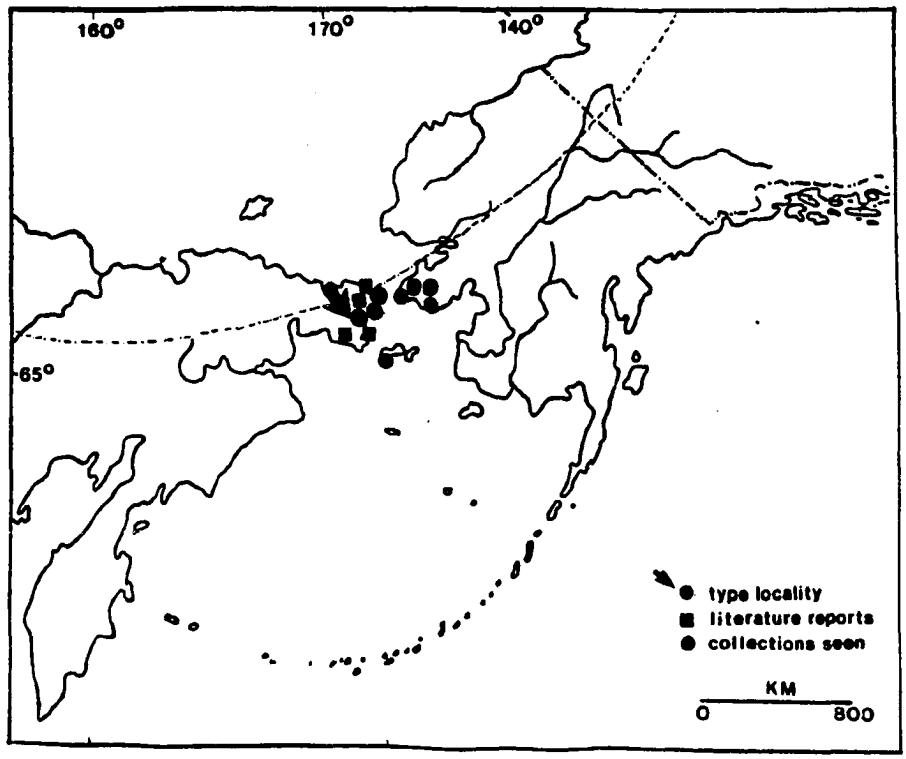


Fig. 2.22. Known range of *Primula tschuktschorum*.

Primula eximia Greene (Fig. 2.23)

Primula eximia Greene, Pittonia 3: 251. 1897. *P. tschuktschorum* subsp. UNITED STATES. ALASKA: St. Paul Island, *Macoun in 1896, 1897* (Lectotype here designated: NDG!-Herb. Green. 18809; Isotypes: BM!, NDG!-Herb. Green. 18791).

P. nivalis var. *pumila* Ledeb., Fl. Ross. 3: 10. 1847. *P. tschuktschorum* var. *pumila* (Ledeb.) Fern., Rhodora 30: 63. 1928. TYPE: U.S.S.R. CHUKOTSK PENINSULA: St. Lawrence Bay, *Chamisso in 1846*. (Holotype: LE?; Isotypes: BM! GH! K!).

P. macounii Greene, Pittonia 3: 251. 1897. TYPE: UNITED STATES. ALASKA: St. George Island, *Macoun in 1897*. (Holotype: NDG! -Herb. Green. 18808; Isotype: US!)

P. arctica Koidzumi, Bot. Mag. (Tokyo) 25: 216. 1911. *P. pumila* var. *arctica* Busch, Fl. Sib. & Orient. Extrem. 4: 75. 1925. *P. tschuktschorum* var. *arctica* (Ledeb.) Fern., Rhodora 30: 63. 1928. TYPE: U.S.S.R. CHUKOTSK PENINSULA: Port Providence, *Yokoyama in 1907* (Holotype: KYO?).

P. pumila var. *ledebouriana* Busch, Fl. Sib. & Orient. Extrem. 4: 75.1925, pro parte. TYPE: Unknown, no specimens listed.

P. tschuktschorum subsp. *cairnesiana* Porsild, Canad. Field Naturalist 79: 87. 1965. TYPE: CANADA. YUKON. Mackenzie Mts., *Gjaerevoll 1055* (Holotype: CAN!).

Plants covered with white farina in youth, usually becoming glabrous with age. Scapes 2-40 cm tall, frequently ascapose at first flowering with scape greatly elongating in age. Leaves variable, lanceolate to elliptical, 0.7-3 cm wide; margins entire to dentate or serrate; petioles winged or obsolete. Involucral bracts lanceolate, 0.2-1 cm long, acute or obtuse at the tip, of unequal width. Umbel (3) 5-20 flowered, blooming asynchronously; pedicels 0.3-3 cm long. Flowers homostylous. Calyx green or greenish-black, 0.5-0.7 cm long, divided nearly to the base with lanceolate teeth. Corolla rose-magenta, tube 1-1.5 cm long at anthesis,

strongly exserted from the calyx; limb to 1.5 cm diam.; lobes entire or slightly emarginate. Stigmas broadly capitate to bilobed, at anthesis located at or just below the annulus; anthers adjacent. Pollen ca 22 µm diam.; exine reticulate, 3-syncolpate. Capsule cylindrical at maturity, to 3 times the length of the calyx. Seeds 1-2 mm long, medium brown, vesiculate. Chromosome number: $2n = 22$ (Alaska: *Kelso 83-288, Martin in 1985*, both at ALA; Johnson & Packer 1968; Northeast Siberia: Zhukova 1966, 1969, 1982; Zhukova & Tikhonova 1971; 1973; Zhukova et al. 1973).

Habitat: late snowbeds along coastal bluffs and ravines, in the mountains in alpine herb and herb-sedge communities on frost-disturbed areas and in streambeds; from sea level to alpine elevations, found at over 1200 m in the Alaska Range.

Range: In the U.S.S.R. from the Chukotsk Peninsula south to Kamtchatka; in North America throughout coastal Alaska between Cape Beaufort and the Aleutian Islands, more rare inland in alpine areas to the Mackenzie Mts. in northwestern Canada (Fig. 2.25).

Representative specimens examined.

USSR. CHUKOTSK PENINSULA. Aramkatchechene Island: *Wright in 1853-1856* (GH, NY); Konyam Bay: *Kjellman 28-30 Jun 1879* (S); Pitlekaj: *Kjellman 2 Jun 1879* (S); St. Lawrence Bay: *Kjellman 20-21 Jun 1879* (S).

UNITED STATES. ALASKA. Alaska Peninsula. Blue Mt.: *Raup 127* (CAN); King Cove, *Eyerdam 1526* (BM, CAS), *Eyerdam 1706* (NY), *Eyerdam 2026* (GH); Shumigan Island, *Moe 71* (ALA); Terror Bay: *Clark 7 Aug 1950* (ALA). Alaska Range. Denali National Park: *Dean 9 Jun 1959* (ALA), *Mexia 2024* (ALA, BM, GH, NY), *Murie 28 Jul 1964* (ALA); Vicinity of Mt. Hayes: *Murray 308* (ALA). Aleutian Islands. Atka: *Eyerdam 1064* (BM, CAN, CAS, K, NY); Akutan: *Jones 9364* (CAS), *Norberg 493* (NY); Unalaska: *Anderson 4255* (ISC), *Chamisso in 1846* (CAS), *Eyerdam 854* (NY), *Hutchinson 362* (BM); Unimak Island: *Eyerdam 1821* (NY), *2026* (CAN, CAS), *Murie 86* (GH). Bering Sea

Coast: Bristol Bay near Lake Chauekuktul: *Roberson 150* (ALA); Goodnews Bay:*Williams 3504* (ALA, CAN); Igiak Bay: *Blurton-Jones 74* (ALA); Pastolik: *Miller 1997* (ALA); Scammon Bay: *Hultén 17 Jun 1961* (ALA, CAS). Bering Sea Islands. Little Diomede: *Porsild & Porsild 1718* (CAN, GH), *Strickland 3 Jul 1977* (ALA); King Island: *Harbo 216* (ALA), *Renner 19-26 Jun 1974* (ALA); Nunivak Island: *Bos 10 Jul 1965* (ALA), *Miller 218c* (ALA), *Palmer 1145* (ALA), *Seim 3 Aug 1965* (ALA), *Anderson 3923* (ALA), *Stewart 201* (NY); St. George, *Colinvaux et al. 156* (GH), *Ferreira in Jul 1947* (ALA), *Macoun 108593, 108594* (CAN), *94286* (CAN, GH, NY); St. Lawrence: *Geist 17 Jul 1931* (CAN, GH, K, NY), *Mason 76-1113* (ALA), *6070* (CAN, CAS, GH, NY), *Stewart 268* (K), *Stewart 279* (NY), *Williams 640* (ISC), *Young 3, 153, 348, 456, 474, 582, 610, 620* (GH); St. Matthew: *Anderson 3995* (ISC), *Beals 88* (ISC), *Gabrielson 8 Jul 1940* (GH), *Harms 5451, 5334* (DAO), *Macoun 106* (NY), *Macoun 11 Aug 1891* (BM, GH), *Rausch 41, 63* (CAS); St. Paul: *Anderson 3689, 4083* (ISC), *Gabrielson 6 Jul 1940* (ALA), *Macoun 93476* (CAN), *9428* (NY, CAN), *94288* (NY), *94289* (NY), *Merriam 7 Aug 1891* (NY), *White in 1879* (NY), *Williams 1141* (ALA). Gulf of Alaska. Chugach National Forest near Crater Lake: *Bente et al. 77-42* (ALA), *Helmstetter 80-370* (ALA); Hagemeister Island: *Pegau 171* (ALA); Kodiak Island: *Gustafson 7325* (ALA), *Smith 179* (CAS). Seward Peninsula. Cape Nome: *Blaisdell in 1900* (GH); Cape Prince of Wales: *Anderson 4979* (ISC), *Kelso 81-182, 83-102A, 83-104, 83-105, 83-291* (ALA), *Kelso et al. 182* (ALA); Deep Canyon Creek: *Kaufman 1* (ALA); Imuruk Lake: *Sieh 23* (ALA); Kigluaik Mts.: *Kelso 84-202* (ALA); Kuzitrin Lake: *Racine 336* (ALA); Nome: *Anderson 3232* (ISC), *Hutchinson 343-48* (K), *Thornton 2136, 2285* (K), Port Clarence: *Scammon 5593* (ALA); Salmon Lake: *Kaufman 12 Jul 1984* (ALA), *Welsh 5902* (ISC, NY), *Williams 1754* (ALA, BM); Solomon River: *Kelso 83-84* (ALA); Teller Rd.: *Kelso 83-275* (ALA), *Parker 319* (ALA). Yukon-Tanana Uplands. Sourdough Creek: *Halliday 325175* (ALA), *Smith 2009* (ALA). White Mountains: *Gjaerevoll 1055* (CAN).

CANADA. YUKON. Mackenzie Mts.: *Cairnes 93324* (CAN). Richardson Mts.: *Calder 30499* (CAN), *34062* (DAO), *Lambert 25* (CAN).

DISCUSSION

Until now, *Primula tschuktschorum* Kjellm. s. lat. (including *P. eximia* Greene) has been considered the only representative of section *Crystallophlomis* Rupr. (formerly called section *Nivales* Pax) in North America. This east Asian section is characterized by a chromosome base number of 11, a single umbel of large magenta flowers, and a basal rosette of lanceolate, somewhat fleshy leaves. The type species of the section is *Primula nivalis* Pallas of central Asia and southern Siberia. It is characterized by a robust habit, a tall efarinose scape to 40 cm high, distylous flowers, and broadly lanceolate leaves with serrate margins.

The first mention of a relative of *P. nivalis* in the Bering Strait region between Alaska and the northeast coast of Asia was made by Ledebour in 1847. He saw "dwarf" plants from St. Lawrence Bay on the Chukotsk Peninsula and allied them with the more robust central Siberian taxon as *P. nivalis* var. *pumila* Ledeb. In 1882 Kjellman described and illustrated in detail a new species, *Primula tschuktschorum*, which was also based on plants from St. Lawrence Bay. The new species was characterized by its delicate habit, small size (less than 10 cm in height), and linear leaves. From the same location Kjellman distinguished collections that he called *P. nivalis*, larger plants with more flowers and wider leaves. He commented that the earlier name var. *pumila* was not well chosen since some St. Lawrence Bay specimens approached the large size of *P. nivalis* found in central Siberia, and he suggested that these larger plants might be an undescribed species. Other authors have attached subspecific epithets to the Bering Strait taxa, but the robust form was not described as a new species until the treatment of Greene in 1897. Greene had been given material collected on St. Paul Island in the Bering Sea that must have seemed unusually large in comparison to the few arctic specimens available to him. To this St. Paul material, Greene gave the name *P. eximia*, the "extraordinary" primrose. Perhaps partially due to the reputation of Greene as a consummate splitter, *P. eximia* was not generally accepted and the name was placed as a synonym of *P. tschuktschorum* s. lat. in subsequent treatments of the Beringian flora.

Since these initial descriptions, the nomenclature surrounding the Bering Straits plants has been confusing. Although no longer considered part of *P. nivalis* (cf. Hultén 1948, 1968), *P. tschuktschorum* s. lat. has been given numerous specific

nomenclatural history of *P. tschuktschorum* only two references to reproductive morphology have been given. Kjellman (1882) clearly showed distylous flowers in his illustration of *P. tschuktschorum* s. str. and Smith and Fletcher (1942) noted the presence of both distylous and homostylous morphs in the complex, but they had insufficient specimens available to pursue the taxonomic significance. Many of the taxonomists who dealt with *P. tschuktschorum* had no field experience in the Bering Strait region and were thus working entirely with herbarium material. Those who had visited the area were limited to the few accessible coastal ports since no road system existed at the time.

My extensive field and herbarium studies on *P. tschuktschorum* in Alaska have made it possible to reassess the taxonomy of the complex. A primary focus of the work was on reproductive biology, in particular the significance of distylous and homostylous morphs.

Detailed observations were carried out on numerous populations of *P. tschuktschorum* s. lat. on the Seward Peninsula of Alaska. It was possible to observe several populations throughout the summer and to note morphological changes over the growing season. In addition, there are now many herbarium specimens available representing the geographic range of the species complex. As a result of these studies, I suggest that, on the basis of reproductive and morphological traits, *P. tschuktschorum* s. lat. should be considered two distinct species: a very restricted distylous one to which the name *P. tschuktschorum* applies, and a more widespread homostylous species that should bear the name *P. eximia* Greene.

Primula tschuktschorum is an endemic to the Bering Strait region between western Alaska and eastern Siberia. It is entirely consistent in morphology, with uniformly linear leaves, few-flowered umbels, dimorphic flowers, and a short corolla tube equal in length to the calyx. The deeply cleft corolla lobes described in a Lawrence Island specimen by Porsild as var. *beringensis* have been seen only in the type specimens and probably represent a local teratological condition. They have no major taxonomic significance. Soviet authors have used the name *P. beringensis* to include all linear-leaved, few-flowered specimens (Tolmatchev & Yurtsev 1980) and thus in their context the name is equivalent to *P. tschuktschorum* Kjellman.

The need to use the name *P. eximia* for the homostylous relative of *P. tschuktschorum* is unfortunate because the type specimen associated with that name is unusually robust and not a good representative of the species. *Primula eximia* is variable in height, number of flowers, and leaf shape, but this variation that has resulted in such an abundance of nomenclature can be attributed to temporal and ecological factors and a presumably high rate of selfing that increases phenotypic differences between populations. *Primula eximia* is consistent in its homostylous flowers, broadly lanceolate leaves, and in the corolla size and shape, with the tube at anthesis 1.5 to 2 times the length of the calyx.

With the distylous members of the complex removed, the variability that was troubling about *P. eximia* lies in leaf size and shape, number of flowers, height, and pedicel length. Like other members of the genus, *P. eximia* shows considerable phenological variation in a number of characters. Plants often begin blooming when ascapose. Throughout anthesis and until the capsules are well formed, the scape continues to elongate. As the capsules develop, the pedicels elongate and stiffen. Young plants of *P. eximia* are densely covered with white farina on leaves and scape, unlike *P. tschuktschorum*, which is always efarinose. This farina on *P. eximia* lessens with age, and capsule-bearing plants are almost totally glabrous. Therefore, much of the variation in height, pedicel length, and amount of farina present seen in herbarium specimens merely reflect phenological conditions.

Primula eximia is very responsive to nutrient availability. The great size of the type specimen from St. Paul Island can at least in part be attributed to the fertilizing effects of the abundant seabird and marine mammal colonies there. The Bering Sea islands are known for the unusual vigor of their plant life (Porsild 1938, 1965). I have noticed a similar effect on populations of *P. eximia* around Cape Prince of Wales. Plants growing on wet, nutrient-poor tundra soils have lighter green leaves, are smaller in stature, and have fewer flowers per umbel. Plants growing on old Inupiaq home sites and around present dwellings are dramatically more robust, with larger darker green leaves and more flowers. These effects can be seen in other plant taxa as well, including *Koenigia islandica* L., *Artemisia tilesii* Ledeb., and *Chrysosplenium tetrandum* (N.Lund) T.C.E. Fries. Dwarf plants of *P. eximia* from Cape Prince of Wales that were brought to Fairbanks and given high doses of

nitrogen-rich fertilizer showed similar vegetative changes. Plants of *P. tschuktschorum* given the same treatment did not respond with any vegetative change. The leaves remained linear and the umbels were few-flowered.

Phenology is closely related to nutrient availability, and flower number in *P. eximia* may to some extent reflect this relationship. As in other members of the genus with multiflowered umbels, blooming is asynchronous. In *P. eximia*, plants that emerge early from snow cover may have a very prolonged period of flowering with some plants exhibiting capsules and buds simultaneously. Plants that do not emerge from snow cover until late in the growing season may never develop more than a few flowers.

A final factor that can explain the interpopulational variability seen in *P. eximia* is the reproductive system. The alpine populations of the species were almost certainly founded by one or a few colonizing individuals that were able to persist due to their selfing abilities. While some of the coastal Seward Peninsula populations can have several hundred individuals, and the asynchronous development of the flowers offers at least the potential for cross fertilization, the homostylous flower structure most likely promotes a high degree of selfing. Within any single population, individual plants of *P. eximia* are generally consistent in their morphology. This would be expected in inbred populations.

Primula eximia is best considered a polymorphic taxon in its vegetative characteristics, but these reflect ecological and temporal plasticity. Two minor geographic trends are apparent: plants from southwestern Alaska tend to show more broadly obtuse leaves with serrate margins, and plants from interior Alaska tend to have more acute lanceolate leaves. These trends are not strong enough to justify infraspecific recognition. The rarity of *P. tschuktschorum* with its apparently inefficient reproductive system is of concern. The species deserves further attention to determine its population status on the Seward Peninsula and Bering Strait islands. If it is as rare as it appears, serious consideration should be given to awarding this endemic Beringian species protected status in Alaska.

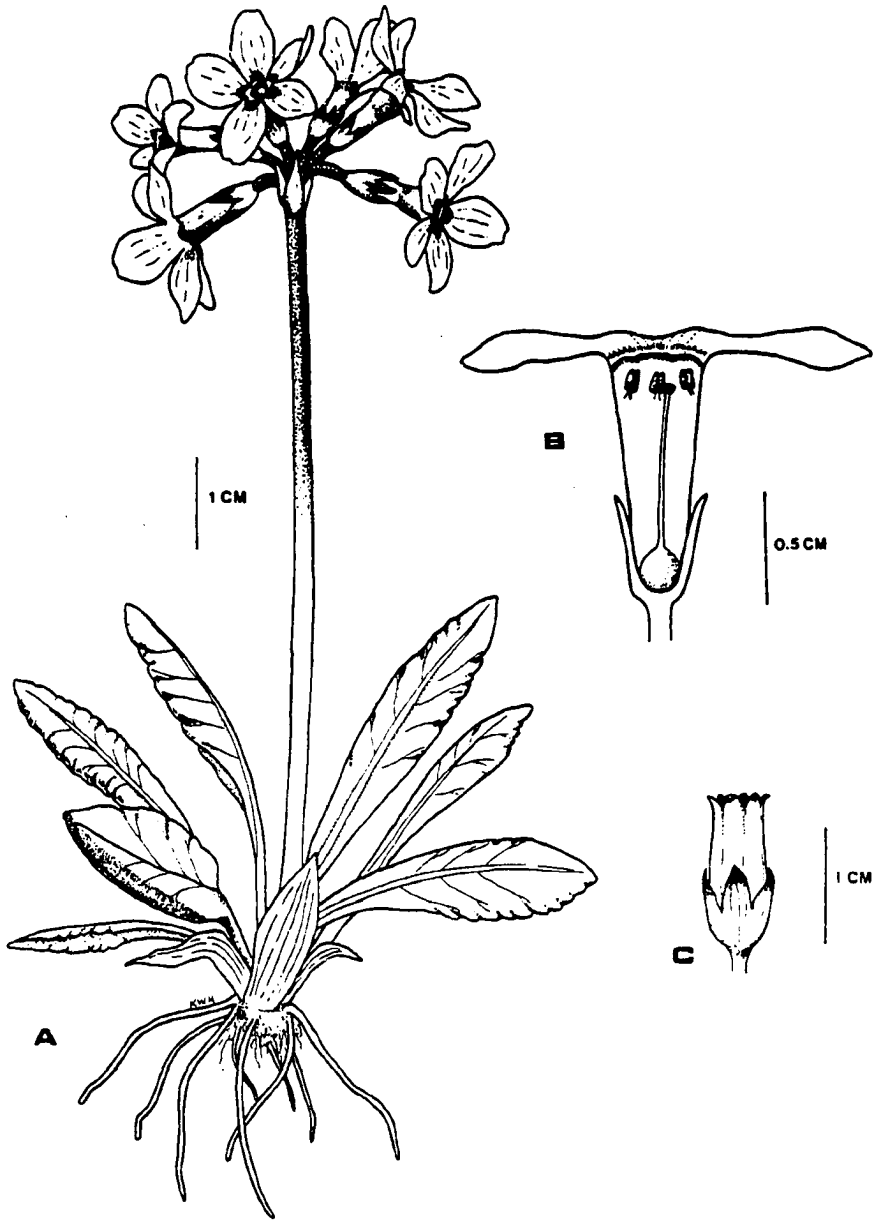


Fig. 2.23. *Primula eximia.* A. Habit. B. Flower. C. Capsule.

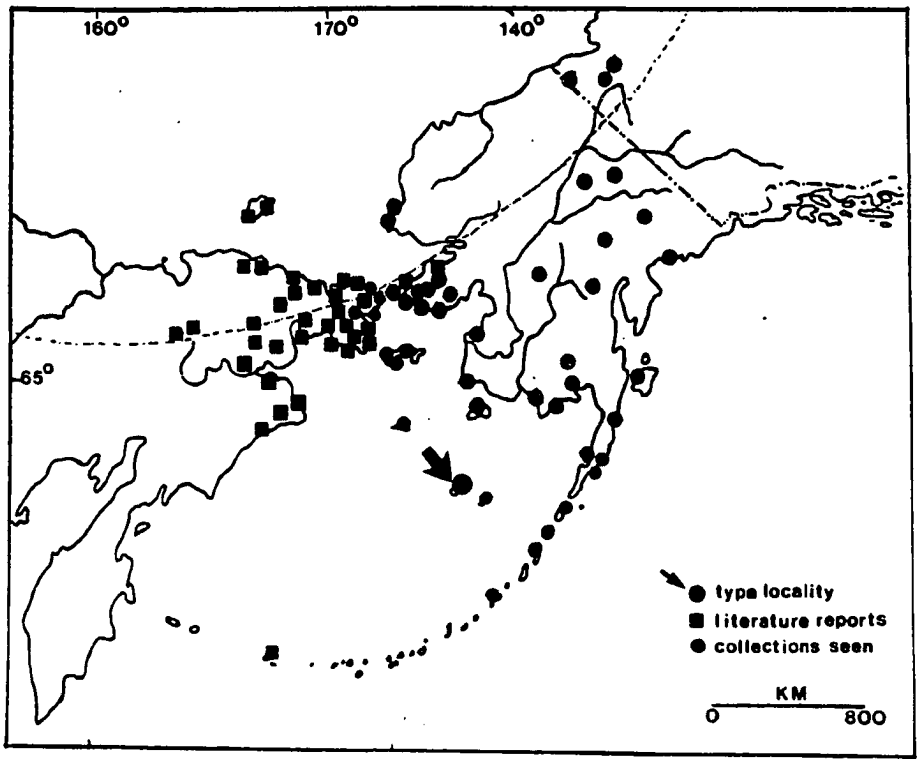


Fig. 2.24. Known range of *Primula eximia*.

Primula section **Cuneifolia** Balfour, J. Roy. Hort. Soc. 39: 178. 1913. TYPE SPECIES: *P. cuneifolia* Ledeb. Leaves with involute vernation; blades cuneate, with coarse teeth, efarinose, with conspicuous glands. Scapes with simple umbels. Flowers rose or magenta; corolla lobes deeply cleft or notched. Chromosome base number: $x = 11$.

Distribution: Japan, NE Asia, Alaska, Sierra Nevada.

North American representatives:

P. cuneifolia subsp. *cuneifolia* (Alaska, NE Asia, Japan)

P. cuneifolia subsp. *saxifragifolia* (Alaska, NE Asia)

P. suffrutescens A. Gray (California)

Primula cuneifolia Ledebour **subsp. *cuneifolia*** (Fig. 2.25)

Primula cuneifolia Ledeb., Mem. Acad. Imp. Soc. St. Petersburg 5:522. 1815. TYPE: U.S.S.R. "in Siberia transbaicalensis".*Tilesius s.n.*? (Holotype: LE?) *P. cuneifolia* var. *Dubyi* Pax, in Engler, Pflanzenreich, Primulaceae 112. 1905. *P. cuneifolia* var. *elongata* Busch, Fl. Sib. & Orient. Extrem. 4:79. 1925.

DESCRIPTION

Plants efarinose with farinipotent glands on vegetative parts, glabrous. Scape to 12 cm high, densely glandular with capitate glands. Leaves including petiole to 6 cm long, 0.8-1 cm wide, broadly cuneate, margins coarsely dentate, blade tapering abruptly to petioles up to 4 cm long. Involucral bracts lanceolate, plane at the base, densely glandular. Umbels 2-9 flowered; pedicels 0.3-0.6 cm long, twice the length of the bracts. Flowers distylous. Calyx green, 0.4-0.6 cm long, urceolate, divided up to 2/3 by lanceolate teeth. Corolla deep pink to rose, rarely white, throat yellow; tube 0.5-1.2 cm long, slightly exserted from the calyx; limb 1.2-2.5 cm broad, deeply cleft. Stamens ca 1 mm long, anthers located near middle of corolla tube in pin plants. Stigma more or less capitate, located in pin plants just above the annulus, positions reciprocal in thrum plants. Pollen dimorphic, in thrum plants ca. 25 μm diam., ca. 20 μm in pin plants, exine microreticulate, 3-syncolpate. Capsule globose at maturity, slightly shorter than the calyx. Seeds brown, 1-1.5 mm long, reticulate, angular with flanged edges. Chromosome number $2n = 22$ (Aleutian Islands: *Friedman 83-3* at ALA; Kamtschatka: Sokolovskaya 1968; Japan: Shimizu 1980).

Habitat: In moist mixed herb meadows with acidic bedrock.

Range: In Alaska, known only from the islands of Attu, Agattu, and Adak in the Aleutian chain. In the USSR, known from the Commander and Kurile Islands south through Kamtchatka to northern Japan (Fig. 2.24).

Representative specimens examined.

UNITED STATES. ALASKA. Aleutian Islands, Adak: *O'Farrell 145* (ALA), *Rausch 28* (CAS); Agattu:*Trapp 23* (COLO); Attu: *Brockner 5* (COLO), *Chandler 29 Jul 1945* (GH),*Coe 28 Jun 1952* (CAS), *Friedman 83-3* (ALA), *Hultén 6790* (CAS),*Trapp 3* (ALA), *Van Schaack 43A, 362* (E), *600, 912* (GH), *Williams 3113* (ALA).

USSR. KAMTCHATKA. *Baynes s.n.* (BM), *Kharkevich s.n.* (COLO), *Kharkevich and Buch 7 Jul 1976* (ALA), *Reider s.n.* (ex. herb. horti. Petropolitani at GH). Akhomten Bay: *Hultén 1237* (GH), Savoiko: *Eyerdam 14 Jul 1928* (GH). SIBERIA. Ajan area: *Baynes s.n.* (BM), *Dov. Piling s.n.* (GH), *Tiling s.n.* (K); Copper Island: *Macoun on 4 Sept 1891* (GH); Commander Islands: *Prebenski s.n.* (E); Kurile Islands: *Barkalov and Naumenko 14 Jul 1978* (GH); Sea of Ochotsk: *Wright in 1853-56* (GH, K).

P. cuneifolia* subsp. *saxifragifolia (Lehm.) Smith and Forrest (Fig. 2.25)

P. saxifragifolia Lehmann, Monograph Primulaceae 89, t.9. 1817. *P. cuneifolia* var. *saxifragifolia* (Lehm.) Pax, in Engler, Das Pflanzenreich, Primulaceae 112. 1905.

P. cuneifolia ssp. *saxifragifolia* (Lehm.) Sm. and Forrest, Notes Roy. Bot. Garden Edinburgh 16:20. 1928. TYPE: UNITED STATES. ALASKA. Aleutian Islands: Unalaska. Collector unknown. (Holotype: LE)

DESCRIPTION

Subspecies *saxifragifolia* differs from subsp. *cuneifolia* in the shorter scape (less than 3.5 cm), shorter petioles (up to 1 cm in length), and the fewer (1-4) homostylous rather than distylous flowers. Chromosome number: $2n = 22$. (*Kelso 85-20* at ALA)

Habitat: Moist herb meadows in the Aleutian Islands with *Anemone narcissiflora* L., *Carex macrochaeta* C.A. Mey., *Hippuris montana* Ledeb., *Lupinus nutkatensis* Donn, *Platanthera dilata* (Pursh) Lindl., *Salix arctica* Pall., and *Viola langsdorffii* Fisch. In the mountains in *Dryas* tundra on gravel frost boils with acidic bedrock; associated species: *Arctous alpina* (L.)Spreng., *Dryas octopetala* L., *Loiseleuria procumbens* (L.) Desv., *Rhododendron lapponicum* (L.)Wahlenb., and *Salix arctica* Pall.

Range: In Alaska found throughout the Aleutian Islands, and along the Bering Sea coast north to the Seward Peninsula, throughout the interior in alpine regions north to Denali National Park, to the south in coastal mountains to northern Vancouver Island (Fig. 2.24).

Representative specimens examined.

UNITED STATES. ALASKA. Aleutian Islands, Adak: *Chandler 20 Jun 1945* (CAS), *Coe 22 Jun 1942* (CAS), *Harms 5283* (COLO), *Rausch 20* (CAS), *Rausch 40* (CAS); Akutan: *Macoun 94290* (GH), *Norberg 305* (K); Amchitka:*Erdman 551* (COLO), *Hutchinson 857* (K), *Reich 215, 343, 449* (ALA); Atka: *Eyerdam 1316* (K), *Eyerdam 933* (K), *Friedman 80-61, 80-73* (ALA); Attu: *Brockner 5* (COLO), *Chandler 18 Jun 1945* (COLO), *Coe 10 Jun 1952* (CAS), *Hardy 87, 88, 225* (CAS), *Hultén 6083* (K), *Schaack 353* (GH), *600* (K), *Soule 175, 305* (K); Unalaska: *Friedman 81-37* (ALA), *Haley 21 Jun 1927, 10-20 Jun 1926* (ALA), *Harrington in 1871* (GH), *Hutchinson 424* , 449 (K), *Langsdorff in 1805* (K), *Nighswonger 1407* (COLO); Unimak: *Eyerdam 1841* (CAS). Alaska Peninsula, Chignik: *Flock 19 Jul 1934* (CAS); Cold Bay: *Cladden in 1924* (CAS); Port Moller: *Haley 11 July 1927* (CAS); Iliamna Bay: *Reed 1206, 1163* (CAS); McNeil River Refuge:*Taggert 12* (CAS, COLO); Port Moller: *Haley 11 Jul 1927* (ALA), Ugaiushuk Island: *Lawhead 137* (ALA). Alaska Range, Copper Mountain: *Mexia 2096A* (CAS); Denali National Park: *Teare 1636* (ALA); Kantishna Hills: *Kelso 85-20, 85-21, 85-22* (ALA); Lake Nerka: *Roberson 468* (ALA); MacLaren Summit: *Rhode 85* (ALA); Mt. Eielson: *Viereck 1165* (ALA, COLO, GH), *Viereck 3214* (COLO); Peters Hills Mountains: *Siplivinsky 806* (ALA); Talkeetna

Mountains: *Helmstetter 110-79* (ALA), *Siplivinsky 806* (ALA). Alexander Archipelago, Juneau: *Anderson 6353* (GH), *Beschel 15427* (COLO), *Lubin 22* (ALA), *Taylor 85* (ALA), *Scammon 1113* (ALA); Prince of Wales Island: *Vorobik 42* (ALA). Bering Sea, Cape Newenham: *Menzies s.n.* (K); Golovin: *Rynning 1025* (ALA); Goodnews Bay: *Williams 3356* (ALA); Izembek Bay: *Murie 30* (GH); Nunivak Island: *Haley 4 July 1927* (CAS), *Miller 215c* (ALA), *Utermohle 32, 132* (ALA); Platinum: *Anderson 12 Jun without year* (ISC); St. Lawrence Island: *Haley 28 Jun 1926* (CAS); St. Matthew Island: *Haley 8 Jul 1927* (CAS); St. Paul Island: *Haley in 1929* (CAS). Chugach Mountains, Hatcher Pass: *Cooper in 1985* (ALA), *Harms 2925* (ALA); Seward: *Calder 5638* (GH), *Cooper 85-10* (ALA); Thompson Pass: *Cooper 85-2* (ALA). Gulf of Alaska, Afognak Island: *Taggert and Zabel 45* (COLO); E. Amatuli Island: *Brainerd 16* (ALA). Kenai Peninsula, Eyak Mt.: *Cooper 85-12* (ALA); Kenai Mts.: *Rice 1147* (ALA); Sheridan Glacier: *Tuthill S10-9* (CAS); Sheridan Mt.: *Cooper 85-10* (ALA). Kodiak Island: *Eyerdam 590A* (CAS, K), *Hutchinson 187* (K), *Loof and Loof 1* (DAO, GH, K), *Smith 178* (CAS). Seward Peninsula, Nome: *Haley 20-27 Jul 1927* (CAS), *Hutchinson s.n.* (E).

DISCUSSION

The Alaskan taxon known as *P. saxifragifolia* was first placed as a subspecies of *P. cuneifolia* by Smith and Forrest (1928), based on their survey of the limited material available from Alaska and northeastern Asia. The nature of the subspecies was then extensively reviewed by Hultén (1937) who concluded that the Aleutian Island taxon described by Lehmann differed only in height, leaf size, and number of flowers. According to Hultén , both subspecies grow in Kamtchatka and on the westernmost Aleutian island of Attu. East of Attu throughout the Aleutian island chain and mainland Alaska, subsp. *saxifragifolia* is found. Hultén retained the subspecific designation of Smith and Forrest for the majority of the Alaskan specimens he examined, and placed most of the material from Kamtchatka and southern Siberia into subsp. *cuneifolia*. The homostylous flowers of subsp. *saxifragifolia* were noticed by Smith and Fletcher (1948) but they were unable to

survey enough Alaskan material to detect if this characteristic was diagnostic of the subspecies.

My examination of material from Alaska indicates that *P. cuneifolia* subsp. *saxifragifolia* is always homostylous. This is the only feature that consistently distinguishes it from subsp. *cuneifolia,* although there are some vegetative characters that can be useful as well. Subspecies *saxifragifolia* tends to be smaller than its Asiatic counterpart. In populations growing on windy ridges, flowers often appear before the scape develops. However, even in these individuals some scape elongation occurs during and after anthesis. In the Aleutian Islands, some individual plants of subsp. *saxifragifolia* can be robust and approach the height of subsp. *cuneifolia* . Subspecies *saxifragifolia* also tends to have shorter petioles than subsp. *cuneifolia,* but there is considerable overlap and this is not a reliable attribute to distinguish between the two subspecies. Flower number is generally fewer in subsp. *saxifragifolia* than in subsp. *cuneifolia.* I have seen no specimens of the former taxon with more than four flowers, while in the latter there can be up to nine flowers.

The Seward Peninsula localities reported in Hultén (1968) for subsp. *cuneifolia* were based on unusually robust forms of subsp. *saxifragifolia.* Hultén was apparently not aware of the distyly/homostyly dichotomy that distinguishes the two subspecies more accurately than vegetative morphology, but with a few exceptions, his determinations were generally correct.

In summary, the morphological differences between the two subspecies are qualitative and overlap considerably. Reproductive biology is the only reliable feature that distinguishes them. In this case, homostyly in itself is not sufficient justification to give recognition at the species level. It is most appropriate, therefore, to follow the nomenclature of Smith and Fletcher (1948b) and treat *P. saxifragifolia* sensu Lehmann as a subspecies of *P. cuneifolia.*

Primula cuneifolia is represented in Japan by two additional subspecies, subsp. *hakusanensis* (Franch.) Smith and Forrest, and subsp. *heterodonta* (Franch.).

Smith and Forrest (Takeda 1913; Ohwi 1965). *Primula cuneifolia* subsp. *hakusanensis* is distinguished by its shallowly denticulate leaves and *P. cuneifolia* subsp. *heterodonta* by its large irregularly dentate leaves. Both Japanese subspecies are distylous.

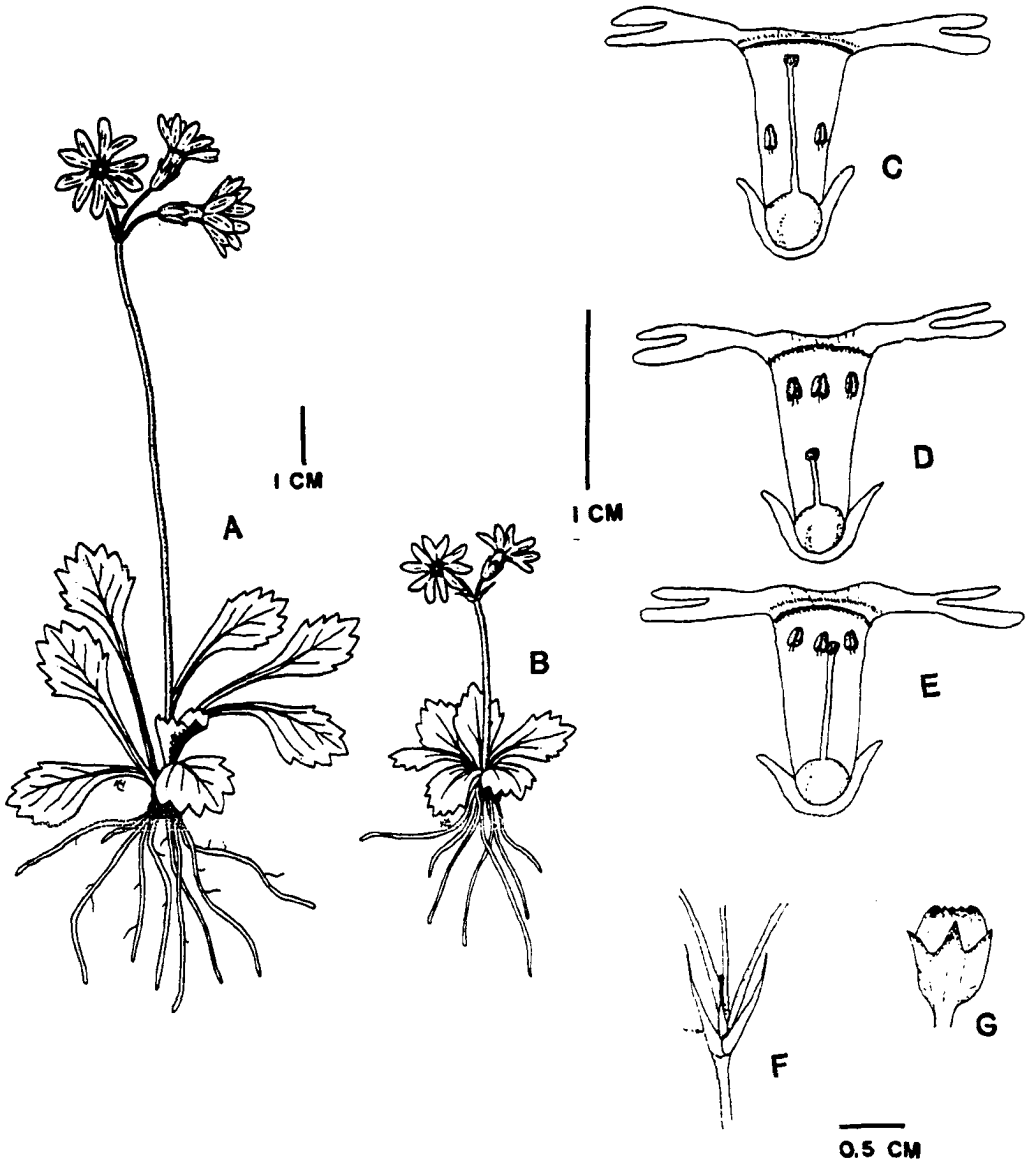


Fig. 2.25. *Primula cuneifolia*. A. subsp. *cuneifolia*. B. subsp. *saxifragifolia*. C. Pin flower (subsp. *cuneifolia*). D. Thrum flower (subsp. *cuneifolia*). E. Homostyle flower (subsp. *saxifragifolia*). F. Bracts. G. Capsule.

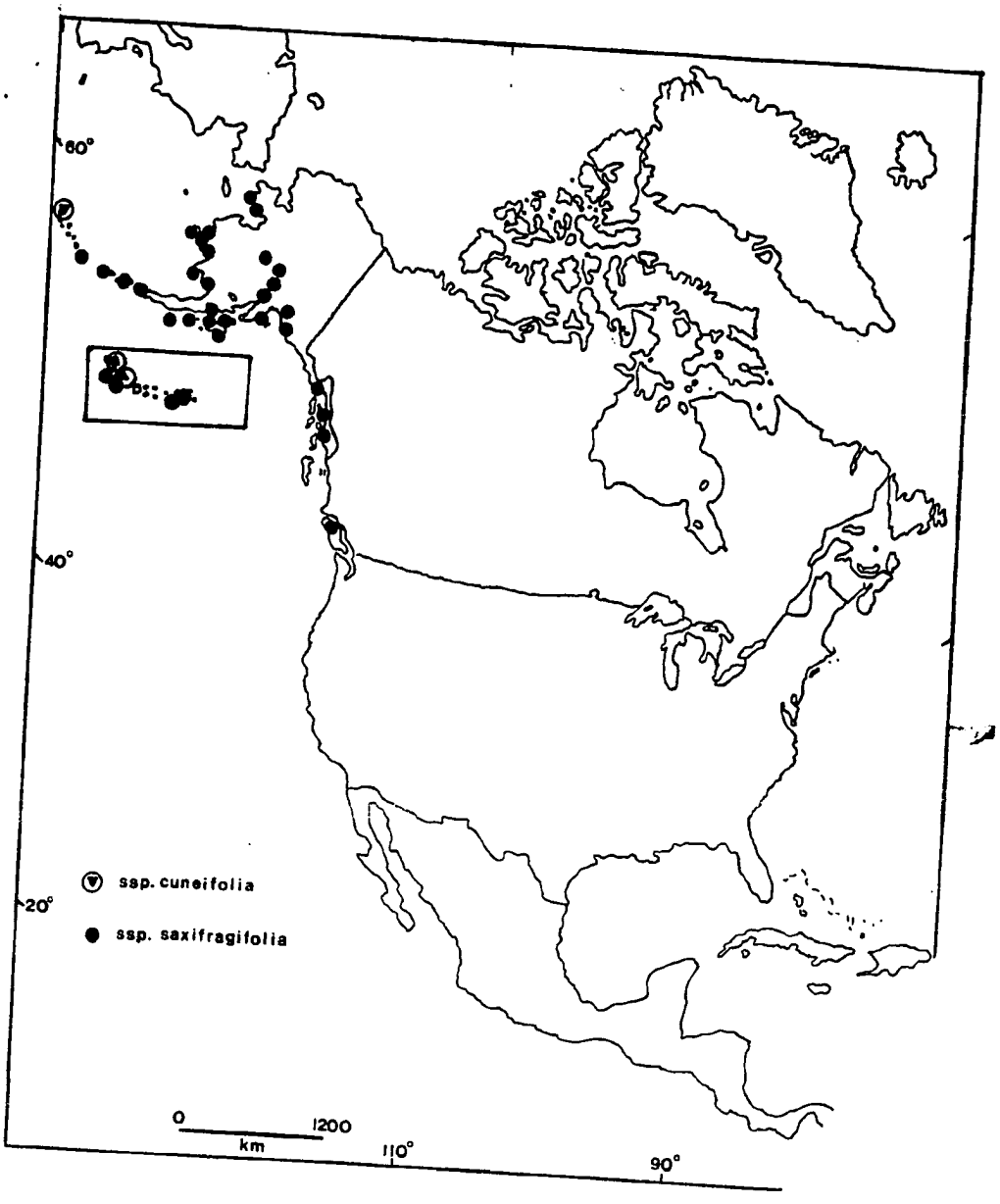


Fig. 2.26. Known range of *Primula cuneifolia* in North America.

Chapter Three
A Phenetic Analysis of the Northern *Primula* Species.

I. Introduction

All of the more than 500 known species of *Primula* bear a strong resemblance to one another. Much of the interspecific variation comes in different combinations of character where small variations in size, color, shape, or ecology can be diagnostic. Even the relatively few species in North America have had a long history of taxonomic confusion. Their resemblance can be attributed both to the morphological conservatism of the genus, and to some close evolutionary relationships as well. In spite of their overall similarity, these *Primula* species are not cryptic, that is, they can be distinguished on the basis of external morphology without having to resort to anatomy or cytology. However, complete modern systematic descriptions have been written for only a small fraction of the species in the genus, and no attempt has ever been made to analyze either sectional relationships or the phylogeny of the genus as a whole by any method other than narrative description.

Overall similarity does not necessarily have to imply a close phylogenetic relationship. However, it is tempting to conclude that species that look alike are likely to be closely related. Most systematists would agree that phenetic groups can at least suggest evolutionary groups. Phenetic clusters based on all possible characters can serve a comparative function for phylogenetic hypotheses. Cladistic methodology provides a counterpart for phenetics in that it selects derived characters for evolutionary analysis, with the intent of creating hypothetical phylogenies. The characters are thus weighted, but clearly some characters *are* more valuable than others in revealing evolutionary relationships. Like phenetic methods, cladistic methods can cluster taxa, too, only the criteria differ. Ultimately, the clusters created by both methods can provide alternatives or serve as supporting evidence for each other.

The drawbacks to cladistic methods are that they are most effective when the characters can be categorized as primitive or derived, and that they require a relatively small and discrete phylogenetic group unless there are a large number of

evolutionarily stable characters to use. It would be a rare species for which the evolutionary state of all the possible phenetic characters could be understood. In a very large genus like *Primula* in which there are few clear synapomorphies, some preliminary phylogenetic divisions might be necessary before cladistic methods could be used. In this case, phenetic approaches can support cladistic ones because they can provide the smaller groups for which detailed character analysis is feasible.

In this sample of fourteen taxa, I believe that the phenetic clusters represent real phylogenetic groups. There is considerable evidence from genetics, ecology, reproductive biology, and biogeography to support this conclusion, and these lines of evidence are discussed in more detail in Chapters 4 and 5.

In this chapter, I apply some techniques of phenetic analysis, using total phenotypic resemblance, to the species of *Primula* found in arctic and boreal North America. The aim of the analysis is to demonstrate that sections of the genus can be effectively delineated and to discuss how a representation of phenetic relationships can contribute to a broader understanding of evolutionary relationships. I make the assumption that each taxon has a standard epiphenotype (Wiley 1981), that is, its own distinctive morphological, genetic and ontogenic nature. Phenetic analysis is not totally objective because it requires that the taxonomist determine and code the taxonomic units and their diagnostic characters. This description of the overall phenotype is a critical first step. Other subsequent steps are less subjective and are relatively standard for a phenetic analysis (see among others, Sneath and Sokal 1973; Dunn and Everitt 1982; Abbott et al. 1985). Here I have used the following techniques:

1. Calculation of a taxon-by-taxon similarity matrix.
2. Cluster analysis of the matrix and presentation of alternative phenograms.
3. Ordination by principal coordinates analysis.

II. Methods and Results.

A. Character coding. The characters used in the analysis were selected after detailed field study and examination of over 2000 herbarium specimens. Eight quantitative and twenty-four qualitative characters were used to describe the phenotype of each taxon (Table 3.1). As far as it was possible to determine, the characters were

sufficiently independent so that no overall factor (for example, a size or ploidy level component) was given excessive weight.

Table 3.1. Characters used in the phenetic analysis of northern species of *Primula*.

1. Mean number of flowers/umbel. 2. Mean pedicel length (mm). 3. Mean corolla width (mm). 4. Mean corolla tube length (mm). 5. Mean calyx length (mm) 6. Mean leaf length (mm). 7. Mean leaf width (mm). 8. Mean scape height (mm). 9. Base number 9 (0) 11 (1) other (2). 10. Leaves distinctly pedicellate (0) leaves not pedicellate (1). 11. Leaf blade lanceolate (0) spathulate (1) elliptical-ovate (2). 12. Leaf margins dentate (0) denticulate (1) entire (2). 13. Base of involucral bracts plane (0) saccate (1) auriculate (1). 14. Bracts involute above (0) plane above (1). 15. Pedicels capillary (0) erect (1). 16. Umbels capitate (0) loose (1) not umbellate (2). 17. Calyx divided <1/4 (0) 1/4-1/2 (1) >1/2 (2). 18. Calyx cylindrical (0) campanulate (1) urceolate (2). 19. Calyx strongly ribbed (0) obscurely ribbed (1). 20. Calyx with green and purple striations (0) calyx green-black (1). 21. Plants heavily farinose (0) somewhat farinose (1) efarinose (2). 22. Glands present on corolla (0) absent on corolla (1). 23. Corolla white (0) lilac (1) lilac or white (2) magenta (3) rose-pink (4). 24. Corolla limb usually entire (0) limb cordate (1). 25. Exine microreticulate (0) reticulate (1) broadly reticulate (2). 26. Colpi none (0) 3 (1) >3 (2). 27. Capsules ovate (0) narrowly cylindrical (1) elliptical (2). 28. Capsule equal to or shorter than calyx (0) slightly exserted to 1.5X length of calyx (1) more than 1.5X length of calyx (2). 29. Seeds reticulate (0) vesiculate (1). 30. Glands capitate (0) capitate/articulated (1) articulated only (2). 31. Corolla tube equal to calyx (0) slightly exserted from calyx (1) more than 1.5X length of calyx (2). 32. Leaves fleshy (0) somewhat fleshy (1) not at all fleshy (2).

The taxonomic units were all at the species level, except for the two subspecies of *P. cuneifolia*. Measurements were made on 11 to 200 individuals of each taxon, depending on the availability of specimens and the variability of the taxon. For most taxa, quantitative measurements were made on at least 60 specimens. Summary statistics of the data and the complete character-by-taxon matrix are given in Appendix 1.

B. Measurement of Similarity. When the diagnostic characters of a taxon are both quantitative and qualitative, the most commonly used coefficient of similarity is that of Gower (1971):

$$S_{ij} = \sum_{k=1}^{p} s_{ijk} \; / \sum_{k=1}^{p} w_{ijk}$$

The weight w_{ijk} is equal to 1 or 0 depending on whether the comparison of taxon *i* and taxon *j* is valid for character *k*. For 2-state characters, scores and weights are coded as in the following example.

Taxon *i*	+	+	-	-
Taxon *j*	+	-	+	-
Score s_{ijk}	1	0	0	0
Weight w_{ijk}	1	1	1	0

For multistate qualitative characters, $s_{ijk} = 1$ if two taxa *i* and *j* are the same for character *k* and 0 if they are different. For quantitative characters, $S_{ijk} = 1 - |x_{ik} - x_{jk}| / R_k$ where R_k is the range of the values possible for character k (here based on the sample in the population under investigation), and x_{ik} and x_{jk} are the values for character *k* in taxa *i* and *j* respectively. Since the same quantitative measurements were available for all taxa, w = 1.

For the hypothetical taxa A, B, C, and D, similarity indices are calculated as shown.

Table 3.2. Data illustrating the use of Gower Similarity Coefficient.

	Farina present	scape hgt.	#flwrs	color	corolla width
Taxon A	+	10 mm	10	red	15 mm
Taxon B	+	7 mm	4	white	8 mm
Taxon C	-	5 mm	3	white	5 mm
Taxon D	+	3 mm	3	red	5 mm

$$S_{AB} = \frac{1 + (1-3/7) + (1-6/7) + 0 + (1-7/10)}{1+1+1+1+1} = .483$$

$$S_{AC} = \frac{0 + (1-5/7) + (1-7/7) + 0 + (1-10/10)}{0+1+1+0+1} = .095$$

Gower similarity coefficients using all 32 characters were calculated for each taxon with the program MIXSIM (Zurcher 1982); the resulting taxon-by-taxon similarity matrix is given in Table 3.3.

Table 3.3. Gower similarity coefficients of 14 taxa of northern species of *Primula*.

1	1.0000													
2	.7913	1.0000												
3	.4727	.5298	1.0000											
4	.4851	.4849	.8961	1.000										
5	.3669	.4582	.3478	.3223	1.0000									
6	.3452	.4453	.3308	.3227	.7108	1.0000								
7	.3154	.3247	.4172	.4452	.3765	.4685	1.0000							
8	.4248	.3722	.4397	.4016	.4022	.4571	.7909	1.0000						
9	.3970	.3194	.3255	.3578	.3825	.4673	.7390	.7876	1.0000					
10	.3920	.3419	.3995	.4516	.4213	.3897	.7946	.8013	.6983	1.0000				
11	.3717	.4734	.5363	.5377	.4776	.4803	.7690	.7976	.6646	.7961	1.000			
12	.4603	.3812	.4307	.3783	.3779	.3449	.6483	.7604	.6011	.6568	.7386	1.000		
13	.4389	.3714	.4424	.5006	.3098	.3605	.7024	.7039	.6807	.7241	.7582	.6616	1.0000	
14	.3467	.4599	.4828	.4799	.4123	.4750	.6820	.6993	.5803	.7047	.8619	.6494	.7931	1.000
	1	2	3	4	5	6	7	8	9	10	11	12	13	14

1 = *eximia* 2 = *tschuktschorum* 3 = *cuneifolia* subsp. *cuneifolia* 4 = *cuneifolia* subsp. *saxifragifolia*
5 = *nutans* 6 = *egaliksensis* 7 = *stricta* 8 = *laurentiana* 9 = *incana* 10 = *borealis* 11 = *mistassinica*
12 = *specuicola* 13 = *alcalina* 14 = *anvilensis*

C. Cluster Analysis. Taxa were clustered by three agglomerative hierarchical methods: average linkage (UPGMA), single linkage (nearest neighbor), and complete linkage (farthest neighbor) using SPSSX (procedure CLUSTER). The phenograms from these three methods are shown in Figs. 3.1, 3.2, and 3.3. A cophenetic correlation coefficient (Sneath and Sokal 1973) was calculated for each

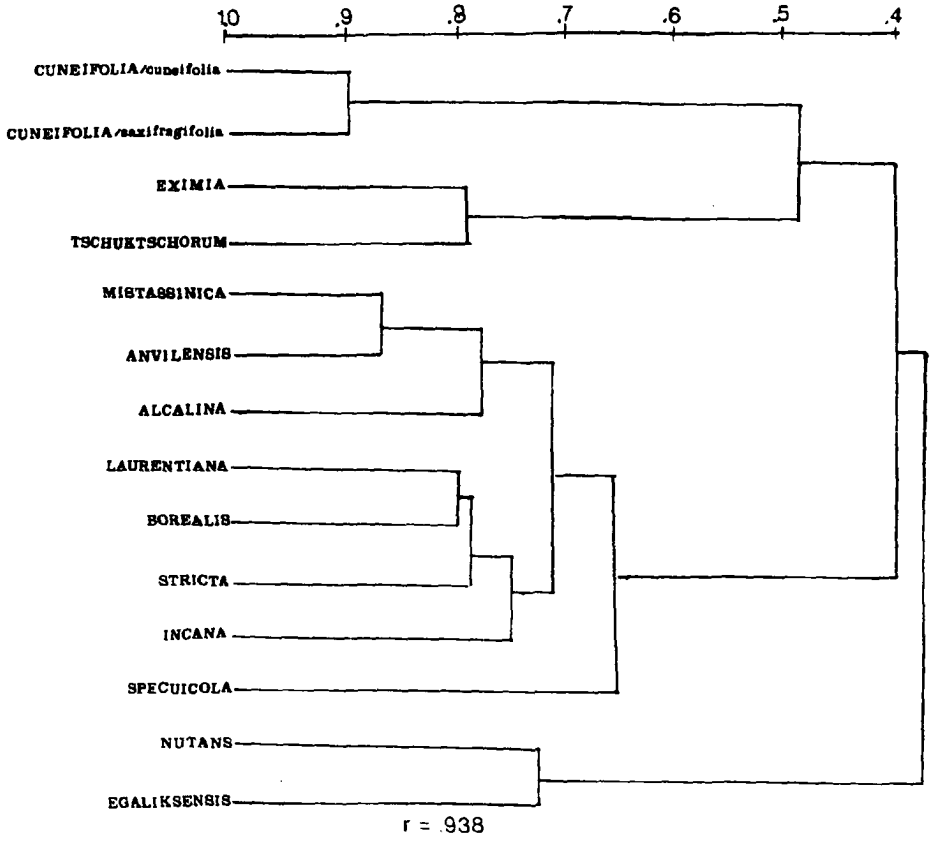


Fig. 3.1. Phenogram of northern species of *Primula* using average linkage clustering. The cophenetic correlation coefficent *r* represents correlation with the original similarity matrix.

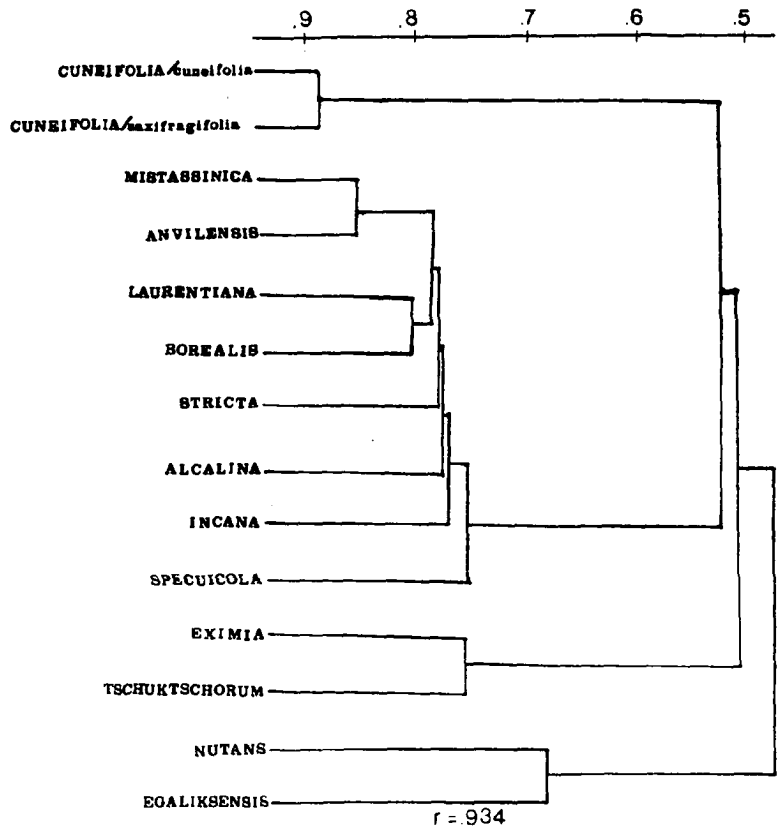


Fig. 3.2. Phenogram of northern species of *Primula* using single linkage clustering. The cophenetic correlation coefficient *r* represents correlation with the original similarity matrix.

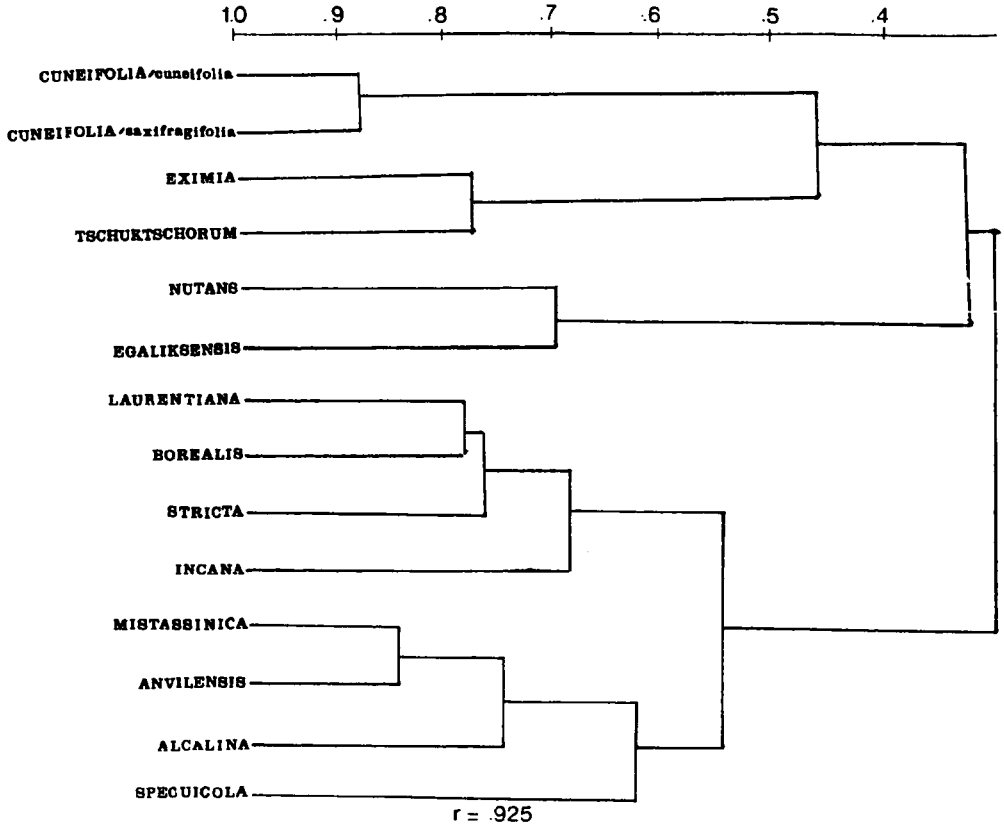


Fig. 3.3. Phenogram of northern species of *Primula* using complete linkage clustering. The cophenetic correlation coefficient *r* represents correlation with the original similarity matrix.

phenogram. This is a measure of how well the similarity matrix implied by the phenogram matches the original similarity matrix. It is computed as a Pearson product-moment correlation coefficient (r) between the original similarity matrix and the matrix created by the clustering algorithm.

D. Ordination: Principal Coordinates Analysis. If a taxon can be adequately described by quantitative data, one commonly used alternative to phenograms for the purpose of portraying taxonomic clusters is to ordinate taxa on first and second principal component axes (Abbott et al. 1985). However, between species of *Primula* there is considerable overlap in the range of quantitative characters so it is necessary to use both quantitative and qualitative data for taxonomic descriptions. Therefore, in this instance ordination of principal component scores is not appropriate. However, Gower (1966) has shown that Principal Coordinates Analysis (PCO) can be used as an alternative to Principal Components Analysis to portray multivariate data. PCO is technically very similar to Principal Components Analysis except that it extracts eigenvalues from a matrix of similarity or distance coefficients rather than from a variance-covariance or correlation matrix. These coefficients can be calculated by any mixed character index. The purpose of principal coordinates analysis is to portray multidimensional distances between taxa in two dimensions in a way that minimizes distortion. The ordination involves plotting the component scores of each variable (i.e. taxon) for the first three principal axes.

From the similarity matrix shown in Table 3.3, eigenvectors with corresponding eigenvalues were extracted using the SPSSX procedure FACTOR (Table 3.4; 3.5). The first three factors accounted for a large proportion of the total variance.

Table 3.4. Eigenvalues of the first three factors extracted from the matrix of similarity coefficients for northern *Primula* species.

	Eigenvalue	% Variance	Cum % Variance
Factor 1	7.90934	56.5	56.5
Factor 2	1.67549	12.0	68.5
Factor 3	1.15961	8.3	76.7

Table 3.5. Eigenvectors of the first three factors of similarity coefficients.

	Factor 1	Factor 2	Factor 3
eximia	.60251	.52413	-.01497
tschuktschorum	.61283	.60306	.08811
cuneifolia	.65406	.49058	-.39056
saxifragifolia	.65613	.45746	-.41979
nutans	.58239	.26748	.61786
egaliksensis	.60907	.19391	.62239
stricta	.83289	-.31254	-.01022
laurentiana	.86704	-.28711	.00553
incana	.78218	-.29072	.09524
borealis	.84235	-.28795	-.03909
mistassinica	.90336	-.16831	-.04477
specuicola	.78965	-.18433	-.06941

Because the first three factors account for so much of the variance, I decided that ordination of the individual factor scores would give an accurate representation of the relative positions of the taxa. Figure 3.4 shows a plot of Factor 1 and Factor 2 scores, Figure 3.5 shows Factor 1 and Factor 3 scores, and Figure 3.6 shows Factor 2 and 3 scores. These plots can be interpreted as different views of the relative positions of the taxa in three dimensional space (Fig. 3.7)

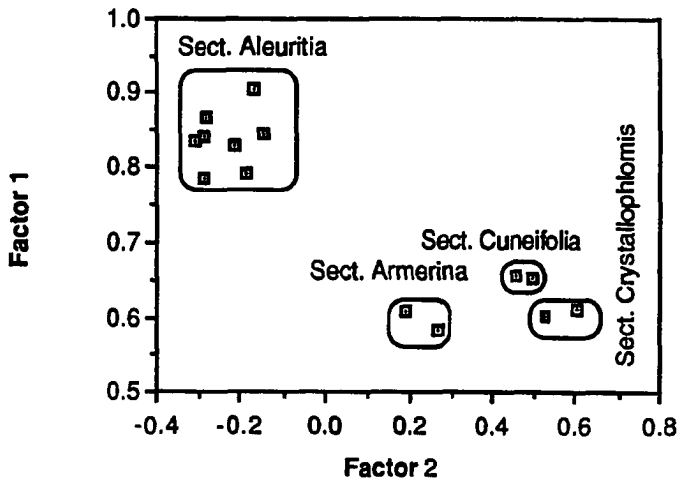


Fig. 3.4. Ordination of Factors 1 and 2.

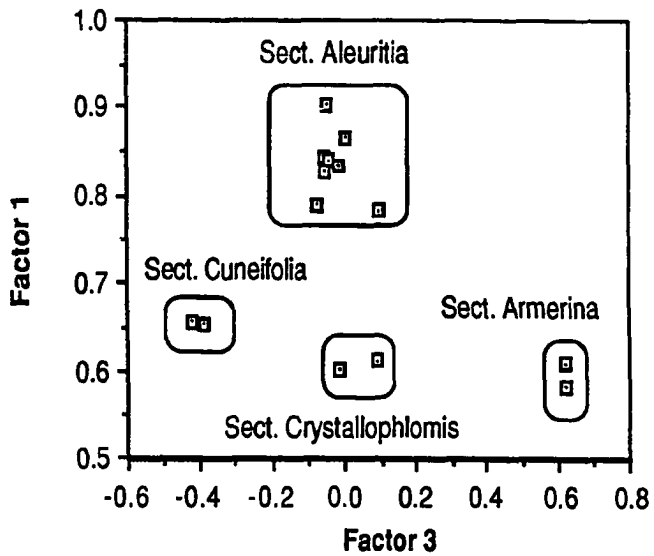


Fig. 3.5. Ordination of Factors 1 and 3.

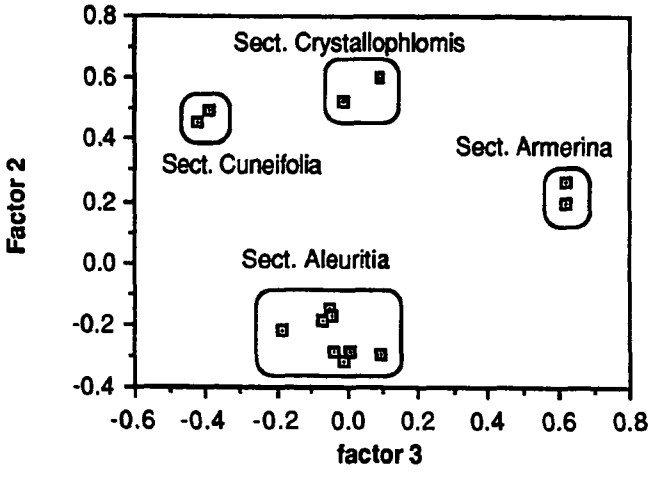


Fig. 3.6. Ordination of Factors 2 and 3.

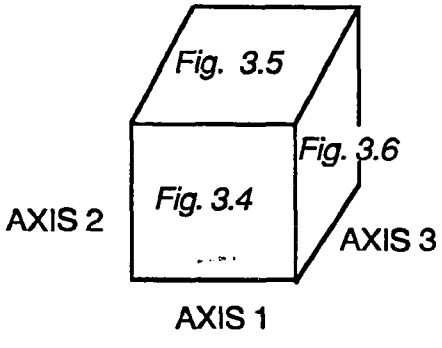


Fig. 3.7. Geometrical interpretation of Figs. 3.4, 3.5, and 3.6.

III. Discussion.

There is very little difference between the results of the three clustering algorithms. In all cases there are four distinct clusters (Figs. 3.1-3.3): one of *P. tschuktschorum* and *P. eximia*, one of the two subspecies of *P. cuneifolia*, one of *P. nutans* and *P. egaliksensis*,

and one of *P. anvilensis, P. alcalina, P. mistassinica, P. specuicola, P. borealis, P. incana, P. laurentiana,* and *P. stricta.* These clusters correspond to currently recognized sections of the genus: *Crystallophlomis, Cuneifolia, Armerina,* and *Aleuritia,* respectively. The high cophenetic correlation coefficient indicates that all three algorithms represent the original similarity matrix well, but that as expected (Farris 1969) the average linkage clustering has the highest correlation coefficient. These four clusters also appear in the ordination of the PCO scores (Figs. 3.4, 3.5, 3.6). Ordination of different factor scores can sometimes reveal patterns that may not be visible in a cluster analysis, but in this case, the patterns are clear in both, and identical in both ordinations and all three of the phenograms.

Traditional taxonomists have been criticized for their gestalt classifications because intuitive clustering, while nominally based on overall phenotype, often reflects unconscious weighting of certain characters. While experienced taxonomic "intuition" should not be ignored, it is sometimes difficult to justify. Certainly the four sections of *Primula* represented by these northern taxa would be distinct to anyone with a familiarity with the genus. It is reassuring, therefore, that here "objective" techniques support intuitive classification. While this numerical analysis does not give any new insights, it does serve the purpose of confirmation, and it is useful as a preliminary step towards applying contemporary systematic techniques to a large, complex, and still taxonomically disorganized genus. Phenetic analysis, whatever its proponents might protest to the contrary, still requires taxonomic judgment and one hopes, skill, in the selection of characters and the definition of taxonomic units. However, it can be appropriate to delineate groups that share overall resemblance, and this introductory analyis suggests it may be useful in identifying sectional relationships in *Primula.*

In summary, phenetic analysis can be an important first step in systematic studies. It requires a determination of all the phenetic characters of a taxon and some understanding of their relationship to each other. It can provide taxonomic groupings for which the evolutionary significance can be judged by other criteria. In these species of *Primula,* phenetic analysis is successful at showing evolutionarily coherent groups that correspond to taxonomic sections of the genus. I suggest that any complete systematic treatment of *Primula* would benefit from an initial phenetic analysis that could clarify all the sectional groups. These can then be subjected to further examination of character change, reproductive biology, ecology, genetics, biogeography, or whatever other lines of evidence become appropriate, to provide a multidimensional phylogenetic portrait of the genus.

Chapter Four

Taxonomic and Biogeographic Implications of Distyly and Homostyly in Northern Species of *Primula*

I. Introduction: distyly and homostyly in *Primula*

The discovery of heteromorphism in the reproductive structures of certain species of *Primula* is attributed to Clusius in the 16th century (Ganders 1979) but the first comprehensive study of the phenomenon was not done until three centuries later by Charles Darwin (1877). Since that time, the genetic and evolutionary background of heterostyly has been examined by a number of investigators (among them, Bateson and Gregory 1905; deWinton and Haldane 1933; Haldane 1938; Mather and deWinton 1941; and Charlesworth and Charlesworth 1979). Recent reviews on the subject have been written by Veuilleumier (1967), Ford (1971), Yeo (1975), Ganders (1979), and Richards (1986).

The term "heterostyly" was coined by Hildebrand (1867) who referred to floral polymorphism in which two or three morphs differ in the placement of style and stamens. In modern usage, the term implies di-allelic genetic control and a concommitant intra-morph sporophytic incompatibility system. There are two types of heterostyly: distyly, with two morphs controlled by a single locus S, and tristyly, with three morphs controlled by two loci, S and M. Both systems are relatively rare. Distyly is known from over twenty unrelated families of angiosperms and is best known in the Rubiaceae, Plumbaginaceae, and Primulaceae. Tristyly is known only from the Lythraceae, Oxalidaceae, and Pontederiaceae (Ganders 1979). While they have some overall similarities, the genetic and reproductive implications of distyly and tristyly are quite different. For this reason, I prefer to use these more precise terms in lieu of the general term heterostyly. Since tristyly is not found in *Primula*, it will not be discussed here (for recent treatments see Barrett 1977, 1979; Charlesworth 1979; Barrett and Glover 1985).

Despite the attention it has received in the last century, some aspects of distyly are still not clearly understood. We do know that there is a syndrome of morphological, anatomical, and physiological attributes that is exhibited in

remarkably similar ways throughout all the families in which it appears. In spite of this similarity, the phylogenetic background of these families is so diverse that distyly must have originated independently several times. Questions about distyly that remain include those that address the evolutionary forces that could have created the uniform syndrome, the adaptive significance of the separate components, the reasons for the breakdown of the complex, and the long term evolutionary significance of the breakdown.

By tradition, the distyly locus is referred to as "S", with two alleles: S and s. The most intensive work on this gene has been done in the genus *Primula* (Ernst 1933, 1955; Mather and deWinton 1941; Mather 1950, Dowrick 1956). In *Primula* (and in all other distylous genera as well) S is treated as a supergene, a tightly linked group of loci which act in unison with only rare crossover events. While a number of possible subunits have been suggested, three have been identified in *Primula* : G/g (style length, stylar conducting tissue, stigmatic papillae type,and female incompatibility), P/p (pollen size and male incompatibility) and A/a (anther position). A heterozygous individual Ss (genotype GPA/gpa) is called a "thrum". It has a short style, with short stigmatic papillae, large pollen, and anthers positioned high in the corolla tube (Fig 4.1a). A homozygous recessive individual ss (genotype gpa/gpa) is called a "pin". It has a long style, long stigmatic papillae, small pollen, and anthers positioned low in the corolla tube (Fig. 4.1b). Due to the accompanying sporophytic incompatibility system, pollen from a pin individual can sucessfully fertilize only a thrum individual, and vice-versa. A homozygous dominant individual should therefore theoretically not occur; if it did, it would be phenotypically a thrum.

Because the subunits are so closely linked, recombination within the S locus is rare. It would occur only in a heterozygous (thrum) individual. Theoretical recombinations are listed in Table 4.1, but the only documented ones are Gpa/ (Gpa, gpa) and gPA/ (gPA,gpa), which all appear as homostyles. Here male and female organs from the pin and thrum morphs are juxtaposed (Fig. 4.1c, d) and thus are entirely self-fertile.

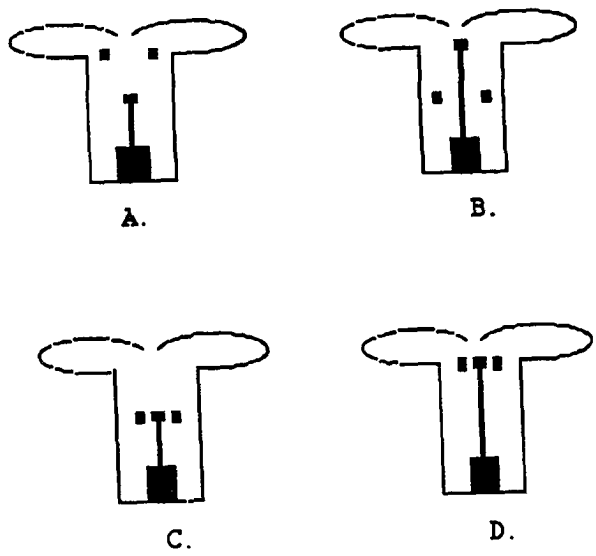


Fig. 4.1. Distyly and homostyly in *Primula*. A. Thrum morph. B. Pin morph. C. Short homostyle morph D. Long homostyle morph.

Table 4.1. Theoretical recombinations within the distyly locus.

Recombinant	Morph with gpa chromosome
GPA	self incompatible thrum
GpA	self compatible thrum
gpA	self compatible long homostyle
gPA	self incompatible long homostyle
gpa	self incompatible pin
gPa	self compatible pin
GPa	self incompatible short homostyle
Gpa	self compatible short homostyle

In the wild, only long homostyle Primulas (genotype gPA/gPA or gPA/gpa) have been found. Richards (1986) suggested three possible reasons for this. First, with the questionable assumption that homostyles produce only selfed seed, long homostyles will produce more long homostyle offspring than short homostyles will produce short homostyle offspring (Fig. 4.2) If the ability to self is advantageous, selection will occur for long homostyles. Second, even if long homostyles may outcross to some extent, short homostyles may not outcross at all due to the protected position of the reproductive organs deep within the corolla tube. This lack of outcrossing may result in inbreeding depression for the short homostyles. Third, pollen germination in short homostyles may be inhibited if the corolla tube fills with rainwater (Eisikowitch and Woodell 1975). Because the anthers in long homostyles are located high in the corolla tube, they may be less affected by this loss of fertility. Whatever the reasons are for the lack of naturally occurring short homostyle morphs, long homostylous morphs are known to occur occasionally in normally distylous taxa while other taxa are always homostylous. For the purpose of this discussion, the term homostyly hereafter refers to the long homostylous morph.

The degree of outcrossing that homostyle primroses undergo has long been the subject of debate. No self-incompatible homostyle *Primula* has ever been documented, and the proximity of anthers and stigma suggests that a very high degree of selfing is possible. While it is generally agreed that homostyle primroses do self, there are no empirical studies to estimate the actual rate of self-fertilization. Piper (unpublished mss.) found no isozyme variability at twelve loci in the homostyle *P. scotica*, so he could not obtain estimates of the rate of selfing. His data at least support the premise that the species is highly selfed. The assumption of Crosby (1949) that homostylous morphs of *P. vulgaris* were 100% selfed was questioned by Bodmer (1958). Crosby later (1959) suggested that selfing rates of 90-95% were more realistic, and the recent work of Piper et al. (1984) supports this figure.

In summary, it seems reasonable to assume that while at least low levels of outcrossing are possible for most homostylous Primulas, the presence of distyly or homostyly has direct implications for the predominant breeding system. Distylous individuals are almost 100% xenogamous. The meticulous breeding experiments of

MALE PARENT (short homostyle)

	Heterozygous		Homozygous	
FEMALE PARENT (thrum)	Gpa	gpa	Gpa	Gpa
GPA	GPA/Gpa thrum	GPA/gpa thrum	GPA/Gpa thrum	GPA/Gpa thrum
gpa	gpa/Gpa homostyle	gpa/gpa pin	gpa/Gpa homostyle	gpa/Gpa homostyle
OFFSPRING:	50% thrum 25%pin 25% long homostyle		50% thrum 50% short homostyle	

MALE PARENT (long homostyle)

	Homozygous		Heterozygous	
FEMALE PARENT (pin)	gPA	gPA	gPA	gpa
gpa	gpa/gPA homostyle	gpa/gPA homostyle	gpa/gPA homostyle	infertile
gpa	gpa/gPA homostyle	gpa/gPA homostyle	gpa/gPA homostyle	infertile
OFFSPRING:	100% long homostyle		50% long homostyle	

Fig. 4.2. Potential offspring of long and short homostyles.

Darwin (1877) demonstrated this, and all contemporary studies have supported his conclusions. While Darwin believed that the morphological manifestations of distyly were responsible for disassortive pollination, contemporary authors have questioned this (Ganders 1979), and most believe physiological incompatibility is the critical factor (Dulberger 1975; Richards and Ibrahim 1982; Stevens and Murray 1982; Fincham 1986) that dictates obligate outcrossing in distylous individuals. In comparison, homostyles are self compatible, and the proximity of the reproductive organs assures a high probability of self-fertilization.

The evolutionary origins of distyly have been the subject of much debate (cf. Vuilleumier 1967; Anderson 1973; Charlesworth and Charlesworth 1979; Richards 1986) and will probably continue to be so. In addition to traditional explanations of selective pressure for outcrossing, recent attention has been given to the potential role of sexual selection in the evolution of heterostyly (Charnov 1982; Casper and Charnov 1982; Taylor 1984), The origins of secondary homostyly are somewhat easier to postulate as there are numerous examples of the breakdown of distylous systems both in the Primulaceae and other families (e.g., Baker 1966; Ganders 1975). These examples indicate that distyly can break down when obligate outcrossing is at a selective disadvantage, such as where there is a pollinator shortage or where an inclement climate curtails pollinator activity. Baker (1955, 1959) pointed out that the ability to self-fertilize is adaptive for colonizing species, and homostyly often occurs in conjunction with successful long distance dispersal. While there are a number of alternative explanations for the evolution of autogamy in general (see Jain 1976), examples of homostylous taxa provide evidence that reproductive assurance can be a major contributor towards successful establishment.

In this chapter I will first comment on the taxonomic implications of distyly and homostyly in *Primula*, then describe the genus with respect to the types of distylous and homostylous taxa found in the arctic and boreal regions of North America. Finally, I will discuss the breakdown of distyly with particular reference to the advantages of self-fertility in northern environments.

II. Influence of distyly and homostyly on the taxonomy of *Primula*.

Throughout the plant kingdom, there are numerous examples of closely related xenogamous and autogamous taxa in which reproductive biology serves as the

principal basis for taxonomic recognition. In *Primula,* distylous and homostylous morphs can have no infraspecific designation (e.g. *P. vulgaris*) if there are no other morphological correlates. In other species, there may be sufficient geographic and/or morphological coherence to the morphs to justify infraspecific recognition. In a few pairs, such strong morphological differences exist that distylous and homostylous taxa are recognized at the species level. Distyly and homostyly can also play more than a nominal role in the taxonomy of the North American species of *Primula.* Because they dictate the predominant breeding system, they can influence characters other than those related to the reproductive organs.

It has been documented a number of times that plant breeding systems have morphological and anatomical correlates (see among others, Solbrig and Rollins 1977; Schoen 1982; Wyatt 1984a, b), and Ornduff (1969) has emphasized the importance of these characters in taxonomy. Table 4.2 lists some taxonomically useful attributes that may be strongly influenced by breeding biology. The implication of the list is that since autogamous taxa do not need to "advertise" to pollen vectors, they can practice reproductive economies. For example, scent and nectar production ceases, and flower size may decrease to bring reproductive organs into proximity.

In the northern Primulas, a comparison of related distylous and homostylous taxa shows a general trend toward compact inflorescence structure, in particular decreased flower size and shortened pedicels in the homostyles (Table 4.3). This is consistent with what has been described in other autogamous taxa. There are, however, some taxa with anomalous features not expected in predominantly selfing organisms. First, many of the homostylous taxa do produce the attractants of scent and nectar that suggest facultative outcrossing. Second, the correlation of compact umbels and homostyly is not perfect. At least one distylous species (*P. alcalina* in sect. *Aleuritia*) has very short pedicels, and one homostylous species (*P. laurentiana* in sect. *Aleuritia*) has long pedicels. This may also represent reproductive compromises or adaptations for a particular pollinator. Third, not all homostylous taxa have reduced flower size. In section *Crystallophlomis,* the homostylous *P. eximia* has a significantly longer corolla tube than its xenogamous relative ($t = 9.8$, $DF = 77.9$, $p < .001$). It is possible that the increased fecundity of the self-fertile homostyle selects for longer corolla tubes to maximize seed production.

Table 4.2. Characteristics of xenogamous species and their autogamous relatives (after Ornduff 1969 and Wyatt 1983).

XENOGAMOUS	AUTOGAMOUS
self incompatible	self compatible
flowers many	flowers fewer
pedicels long	pedicels shorter
sepals large	sepals shorter
petals large	petals shorter
petals emarginate	petals entire
nectaries present	nectaries reduced
flowers scented	flowers scentless
nectar guides conspicuous	nectar guides absent
anthers long	anthers shorter
anthers extrorse	anthers introrse
anthers distant from stigma	anthers close to stigma
pollen grains many	pollen grains few
pistil long	pistil shorter
style exserted	style included
many ovules/flower	few ovules/flower
some fruits not maturing	all fruits maturing
distribution narrow	distribution wide

Table 4.3. Comparative sizes of distylous and homostylous taxa. Numbers represent overall means measured in mm.

	Pedicel Length(sd)	Corolla Tube Length(sd)	Corolla Limb Width(sd)	#Flowers(sd)
Sect. *Aleuritia*				
Distylous				
P. anvilensis (2x)	6.9 (3.6)	3.0 (1.6)	7.0 (1.5)	3.1 (1.6)
P. alcalina (2x)	3.1 (1.5)	4.9 (0.7)	9.1 (1.0)	7.0 (1.7)
P. specuicola (2x)	21.0 (9.9)	10.9 (2.1)	11.2 (3.2)	12.0 (5.6)
P. mistassinica (2x)	9.9 (6.6)	6.1 (1.0)	10.9 (1.8)	3.2 (2.0)
P. borealis (4x)	4.7 (2.0)	6.9 (1.4)	13.2 (2.2)	4.2 (1.9)
all distylous spp.	9.6	6.4	10.2	5.9
Homostylous				
P. incana (6x)	5.4 (3.9)	7.0 (1.2)	5.2 (1.3)	8.5 (3.9)
P. laurentiana (8x)	6.4 (4.4)	7.6 (0.9)	11.7 (2.7)	5.4 (2.3)
P. stricta (14x)	3.1 (1.4)	6.3 (0.9)	6.2 (1.5)	3.6 (1.5)
all homostylous spp.	5.0	6.7	7.7	5.8
Sect. *Armerina*				
Distylous				
P. nutans (2x)	13.2 (6.4)	8.5 (2.0)	13.3 (2.3)	2.2 (0.9)
Homostylous				
P. egaliksensis (4x)	6.1 (4.0)	5.9 (0.9)	4.9 (1.6)	3.0 (1.1)
Sect. *Crystallophlomis*				
Distylous				
P. tschuktschorum (2x)	6.8 (2.9)	8.3 (1.5)	18.3 (4.4)	1.6 (0.7)
Homostylous				
P. eximia (2x)	7.5 (4.9)	11.7 (1.8)	16.1 (3.6)	5.1 (2.3)
Sect. *Cuneifolia*				
Distylous				
P. cuneifolia subsp. cuneifolia (2x)	6.8 (4.2)	8.4 (2.1)	20.9 (4.4)	2.8 (1.3)
Homostylous				
P. cuneifolia subsp. saxifragifolia (2x)	3.3 (2.5)	6.7 (1.1)	15.3 (3.5)	2.1 (1.3)

Finally, in both section *Aleuritia* and section *Crystallophlomis*, there is a trend towards increased rather than decreased flower number in the homostylous taxa. This may represent a shift in reproductive allocation when pollen availability is no longer a limiting factor for seed production. That is, with homostylous flowers it may be energetically more efficient to maximize successful seed production by increasing flower number rather than by increasing the number of seeds per flower. Alternatively, increased flower number may be part of a balanced breeding system in which mass display attracts insects and sequential flower development promotes cross-pollination (section C below).

For the most part, the Primulas of northern North America fit the morphological models proposed for outcrossing and selfing species. The most important point to emphasize is that in *Primula* the morphological featues we use to define taxonomic boundaries may be strongly correlated with the breeding system. However, the morphology of any taxon reflects the influence of all the ecological factors, both biotic and abiotic, to which the taxon is subjected, as well as the genetic heritage of that taxon. Consequently, not all taxa will exhibit the textbook examples of typical outcrossing and inbreeding morphology. The most meaningful future work may be to ascertain what genetic and ecological forces create apparent compromises between outcrossing and selfing. In addition to an examination of external morphological changes, it would be of great interest to compare relative fertility, pollen/ovule ratios, degree and type of heterozygosity, and actual outcrossing rates of the distylous and homostylous species of *Primula*. Not only is there a dearth of empirical data about how the breakdown of distyly may affect these measures of reproductive and genetic diversity, but also such information could greatly enhance our understanding of the selective forces that have led to diversification of the genus in the arctic.

III. Distribution of distyly and homostyly in northern species of *Primula* : an overview.

A. Distyly.

Each of the four sections of the genus *Primula* under examination contains at least one distylous taxon (Table 4.3).

All the distylous species are diploid except one, *P. borealis* in section *Aleuritia*, that is tetraploid. Four of the Alaskan species were examined in order to certify that these taxa, which are clearly dimorphic in their gross morphology, met the anatomical criteria for distyly as well. In addition, morph ratios in several populations were counted to determine if pins and thrums were in the equal numbers expected for distylous species. It was not possible to survey all the distylous taxa in detail, but there was no indication that any of the criteria of distyly might not be met.

Scanning electron microscopy shows that the stigmatic papillae of the four distylous taxa are dimorphic (Fig. 4.3) As expected, pin morphs have long papillae and thrum morphs have short papillae.

Pollen measurements indicate that all the distylous taxa have two size classes of pollen. Pin pollen is consistently smaller than thrum pollen (Fig. 4.4). This is typical of most distylous taxa (Ganders 1979).

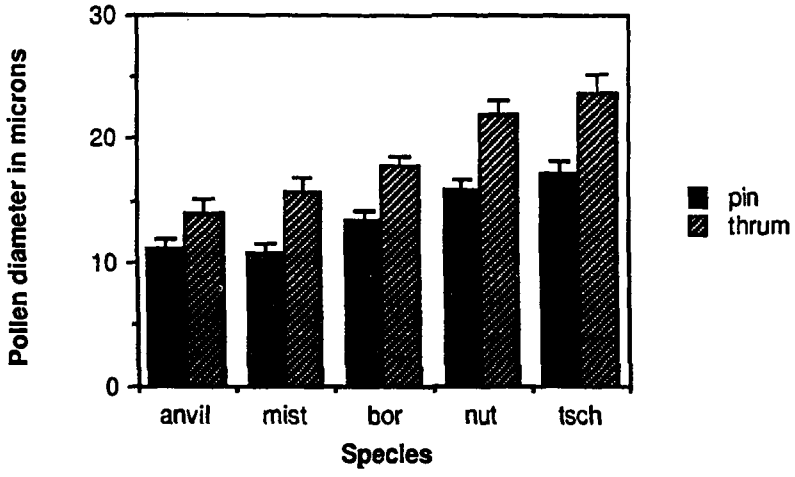


Fig. 4. 4. Pollen sizes in northern species of *Primula*.

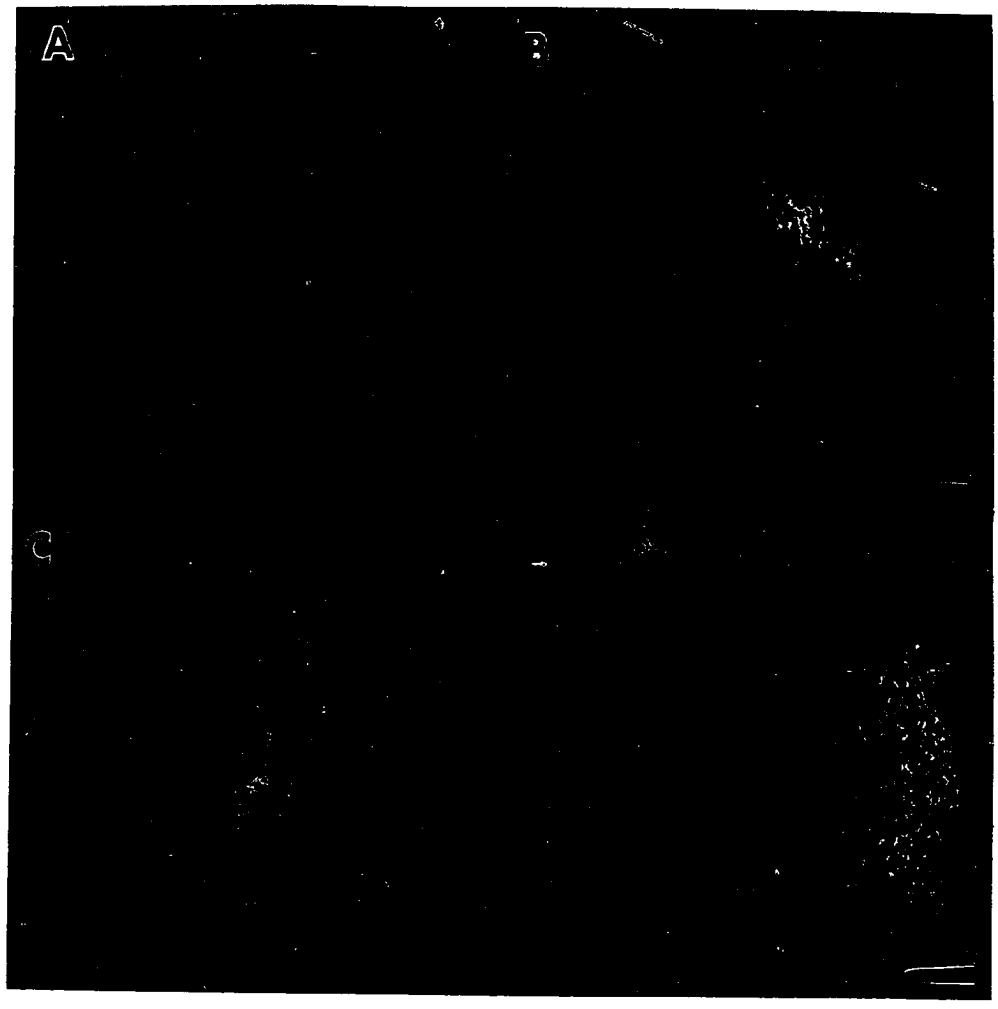
Fig. 4.3. Scanning electron micrographs of stigmatic papillae in distylous species of *Primula*. Scale bar represents 25 μm.

A. *P. tschuktschorum*, pin morph. *Kelso 83-103* (ALA).

B. *P. tschuktschorum*, thrum morph. *Kelso 83-103*.

C. *P. borealis*, pin morph. *Kelso 83-164* (ALA).

D. *P. borealis*, thrum morph. *Kelso 83-164*.



Morph ratios were calculated in six populations representing *P. anvilensis, P. borealis,* and *P. tschuktschorum.* Table 4.4 shows that two populations of *P. anvilensis* deviate from the expected equal number of pins and thrums, but that the other four species do not.

Table 4.4. Number of pins and thrums in Seward Peninsula populations of distylous taxa. Chi-Square statistic tests departure from expected 1: 1 ratio.

	Pin	Thrum	Chi-square	p
tschuk.-1	23	22	0.022	.8815
anvilensis -1	48	29	4.688	.0304*
anvilensis -2	42	25	4.313	.0378*
anvilensis -3	31	33	0.062	.8026
borealis-1	27	32	0.424	.5151
borealis-2	19	20	0.050	.8231

The skewed ratio in populations 1 and 2 of *P. anvilensis* may be attributed to the small size of the populations. Because they were from highly frost-disturbed areas, they may not have reached equilibrium. The northern species of *Primula* often have clumped distributions of morphs due to the tendency for whole capsules to break off and germinate in situ. At these low population numbers, the presence of a few successful clumps could statistically skew the morph ratios. These two slightly anomalous populations are not sufficient evidence to reject the premise that overall morph ratios in distylous populations at equilibrium are approximately equal.

Based on all the above evidence, I conclude that the apparently distylous species of *Primula* have all the anatomical and morphological manifestations of the syndrome. There is no reason to suppose intra-morph incompatibility is not present as well. Due to logistical difficulties in carrying out field experiments on plants that grow in remote places and a lack of greenhouse facilities that could reproduce arctic growing conditions, no statistically valid breeding results are available for the distylous taxa. However, none of the individual plants of *P. anvilensis, P. borealis,* or *P. nutans* that were bagged with insect excluders set any seed, so

presumably incompatibility is as strong in arctic species of *Primula* as it is in temperate ones.

B. Homostyly at the diploid level.

In northern primroses there are two examples of distylous and homostylous pairs at the diploid level. One of these pairs, *P. tschuktschorum* and *P. eximia*, I recognize as separate species. The other pair involves the two subspecies of *P. cuneifolia*, subsp. *cuneifolia* (distylous) and subsp. *saxifragifolia* (homostylous). Other than their reproductive systems, these taxa differ only qualitatively in some vegetative characters and are thus recognized at the infraspecific level only. As a number of authors have shown (e.g. Baker 1955, Stebbins 1957; Wyatt 1983), in selfing/outcrossing pairs, the selfer is almost always the derived taxon. Based on their evidence, it is reasonable here to regard *P. cuneifolia* subsp. *cuneifolia* and *P. tschuktschorum* as the distylous progenitors and *P. cuneifolia* subsp. *saxifragifolia* and *P. eximia* as homostylous derivatives.

The taxonomy of *Primula tschuktschorum* and *P. eximia* (sect. *Crystallophlomis*) was discussed in Chapter 2. The reasons for splitting *P. tschuktschorum* s. lat. at the species level are not only based on reproductive biology, but on consistent morphological attributes as well.

Primula tschuktschorum is an apparently rare endemic of the Bering Strait region in Alaska and the USSR. It has few-flowered umbels of distylous flowers with relatively short corolla tubes. Vegetatively, plants have short delicate scapes and linear leaves. In comparison, the homostylous *P. eximia* is found throughout the Bering Sea region and has spread into the mountains of interior Alaska and the Yukon. Plants are robust, with broad leaves on tall thick scapes, numerous flowers, and a relatively long corolla tube.

Unlike the situation with *P. cuneifolia* where the only reliable difference between the taxa is the reproductive biology, there is significant morphological differentiation between *P. tschuktschorum* and *P. eximia*. There is a dramatic increase in size, flower number, and length of the corolla tube in the homostylous taxon as well as increased size and vegetative production.

In addition, *Primula eximia* is herkogamous for a period of several days. This is not seen in any of the other northern homostylous taxa. In the small-flowered *P. incana*, for example, anthers and stigma are in contact throughout the entire period of

anthesis, leading almost inevitably to a high degree of self-fertilization. In contrast, in *P. eximia* during early anthesis the stigma is considerably above the anthers. Over the next few days, the corolla tube elongates, the attached anthers move up, become adjacent to, and then slightly above the stigma (Fig. 4.5a-c). As in other homostylous taxa, blooming is asynchronous, so a population contains flowers at different stages of growth at any one time. This combination of herkogamy and asynchrony suggests increased opportunity for outcrossing. Additional adaptations for cross pollination include copious nectar production and a strong scent. Interestingly, neither nectar nor scent is as apparent in *P. tschuktschorum,* although this may be attributed to the limitations of human sensitivity and the timing of observations.

Although *Primula eximia* is homostylous, and thus presumably capable of a high degree of self-fertilization, its large flowers, increased size of the inflorescence, nectar and scent production, asynchronous blooming, and initial separation of reproductive organs are all features associated with outcrossing. Furthermore, it is noteworthy that these are features *not* exhibited by the putative progenitor, the distylous *P. tschuktschorum.* It is possible, then, that these represent new adaptations derived from conflicting selective pressures. The work of Barrett and Shore (1987) supports this suggestion. They describe de novo adaptations for outcrossing (including spatial separation of anthers and stigma) in the homostylous derivative of the distylous species *Turnera ulmifolia* L. This is one of the first well-documented examples to indicate that a reproductive switch to predominant self-fertilization need not be an evolutionary dead end. While it still seems safe to conclude that most selfing taxa (including homostyles) are derived from their outcrossing relatives, we should, perhaps, question the assumption that they always are, and document more examples of outcrossing/selfing pairs.

Whether it is due to autogamy alone or the combination of autogamy plus facultative outcrossing, *P. eximia* clearly has a more successful breeding system than *P. tschuktschorum.* Because of concern about damage to the few populations known of *P. tschuktschorum,* extensive reproductive surveys were not carried out on that species. However, observations indicate that seed set is much lower than in *P. eximia* (Table 4.6).

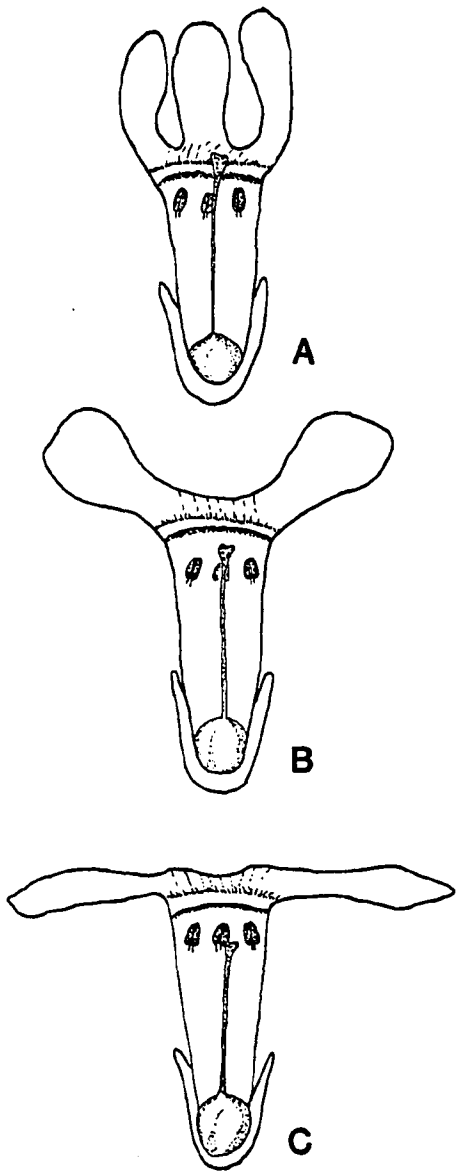


Fig. 4.5. Developmental changes in a flower of *Primula eximia*.

A. Day 1. Flower first opens and stigma is several millimeters above anthers.

B. Day 2. Corolla tube elongates; reproductive organs become closer.

C. Day 3 to end of anthesis of individual flower (ca day 5). Corolla tube continues to elongate and anthers move adjacent to or slightly above stigma.

Table 4.5. Comparative seed set in *P. tschuktschorum* and *P. eximia.* (Data from plants at Cape Prince of Wales, Alaska).

SPECIES	PLANT #	MEAN NO. SEEDS/CAPSULE (SD)
tschuktschorum	1 (n = 2)	<50
	2 (n = 2)	0
	3 (n = 1)	<50
	4 (n = 1)	<20
	5 (n = 2)	<30
eximia	1 (n = 4)	136.3 (21.7)
	2 (n = 4)	93.3 (6.7)
	3 (n = 4)	44.0 (25.8)
	4 (n = 3)	120.3 (19.4)
	5 (n = 4)	80.3 (21.8)
	6 (n = 4)	93.5 (9.0)
	7 (n = 4)	111.0 (16.3)
	8 (n = 4)	104.7 (37.6)
	9 (n = 4)	138.3 (26.3)

None of the populations of *P. tschuktschorum* observed on the Seward Peninsula had more than fifty individuals, whereas for *P. eximia,* population numbers are almost always in the hundreds. The narrow geographic range of *P. tschuktschorum* in comparison to that of *P. eximia* (Fig. 4.6) is further indication that in this case, distyly is not an efficient method of reproduction and that the future of *P. tschuktschorum* may be in jeopardy.

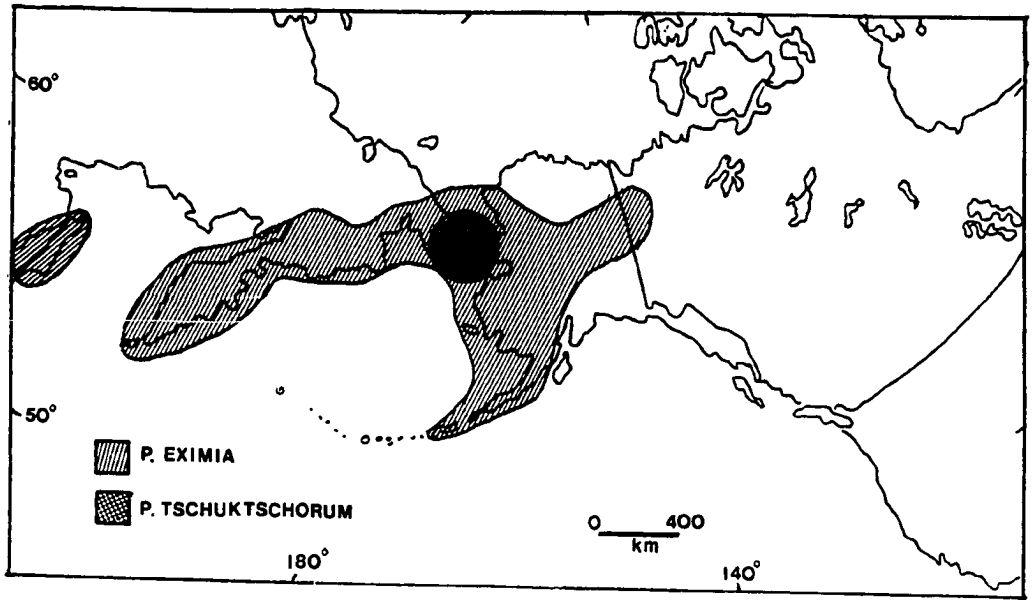


Fig. 4.6. Range of *Primula tschuktschorum* and *P. eximia*.

C. Homostyly at the Polyploid Level.

Brown (1930) was the first to point out the correlation between homostyly and polyploidy. In *Primula,* section *Aleuritia* has a wide spectrum of ploidy levels both in North America and in Eurasia and is the best example of this trend (Table 4.6).

Table 4.6. Distyly, homostyly and polyploidy in *Primula* sect. *Aleuritia.* (After Fenderson 1986 and Richards 1986).

SPECIES	PLOIDY	REPRODUCTIVE SYSTEM	LOCATION
P. alcalina	2	Distylous	Idaho
P. anvilensis	2	Distylous	Alaska
P. mistassinica	2	Distylous	Boreal N. America
P. specuicola	2	Distylous	Utah, Arizona
P. farinosa	2	Distylous	Europe, Asia
	4	Homostylous	Gotland: Sweden
P. frondosa	2	Distylous	Bulgaria
P. longiscapa	2	Distylous	Turkey
P. exigua	2	Distylous	Bulgaria
P. modesta	2	Distylous	Japan
P. daraliaca	2	Distylous	Caucasus: USSR
P. borealis	4	Distylous	Alaska, Siberia
P. halleri	4	Homostylous	Alps, Balkans
P. scotica	6	Homostylous	N. Scotland
P. incana	6	Homostylous	Alaska to Colorado
P. laurentiana	8	Homostylous	E. Canada
P. magellanica	8	Homostylous	Patagonia
P. capitellata	8	Homostylous	Afghanistan, Iran
P. scandinavica	8	Homostylous	Scandinavia
P. stricta	14	Homostylous	E. Arctic

It can be seen that diploids tend to be distylous, tetraploids can be distylous or homostylous, and all taxa over 4x are homostylous. In North American Primulas, *P. borealis*, a tetraploid, is distylous, while *P. incana* (hexaploid), *P. laurentiana*

(octoploid), and *P. stricta* (deca-tetraploid) are all homostylous.

Primula incana is a native of the Fairbanks area and it was possible to bag individual plants with insect excluders in order to check if this species is self-compatible and self-pollinating. The results (Table 4.7) show no difference in seed set between bagged and open individuals.

Table 4.7. Seed production in *P. incana* (unpaired 2 sample t-test).

	Mean #Seeds/Capsule(SD)	#Plants
Open	174 (77.5)	5
Bagged	164 (74.1)	5
	t = .209	
	p > .4 (ns)	

P. incana is obviously both self-compatible and highly fecund. Campbell et al. (1986) found self-compatibility in *P. laurentiana,* and there is no reason to suspect that *P. stricta* does not self-fertilize as well.

While self-compatibility can be assumed for these homostylous species, they show some features adaptive for insect attraction. All have a strong scent, all retain a yellow corolla throat contrasting with violet lobes, and all produce nectar. Campbell et al. (1986) investigated the reproductive biology of *P. laurentiana* and noted visitation by several species of insects, and potential pollination by bumblebees and syrphid flies. It is likely that most of the northern homostylous Primulas have at least low levels of cross pollination through insect visitation.

Mosquin (1966) pointed out that many arctic and boreal taxa *do* show features promoting outcrossing and features promoting genetic constancy through selfing. He commented that these opposing combinations can be explained as adaptations for balanced breeding systems, or, in his view, the more likely alternative is that the features promoting outcrossing are relictual. In the case of the homostyle primroses, both scent and nectar are energetically expensive products to produce, and thus if they did not have an adaptive function would be soon selected against. It seems likely that these features are not simply vestiges of an ancestral breeding system, but rather serve a currently adaptive function for outcrossing.

For some of the homostylous Primulas, biochemical attraction may be

reinforced by inflorescence structure. *Primula incana, P. stricta,* and *P. laurentiana* all have many-flowered umbels. This in itself may serve as an effective insect attractant (Willson 1983) through mass display. Furthermore, the potential for xenogamy can be enhanced by sequential flowering within umbels. At least during the early period of anthesis when only a few flowers are in bloom in any single inflorescence, insect visitors would have a high probability of carrying pollen between plants. With asynchronous flower development, one umbel can remain in bloom for a relatively long period of time (up to several weeks in *P. incana*) in comparison to the distylous species with few-flowered umbels.

The other homostylous species of *Primula* in boreal North America is *P. egaliksensis* of section *Armerina.* It is a tetraploid ($2n = 36, 40$), probably derived from segmental allopolyploidy and aneuploidy from *P. nutans* ($2n = 22$) and the diploid ($2n = 18$) *P. mistassinica* in section *Aleuritia* or an extinct ancestor similar to it (Chapter 5). Unlike the other polyploid homostyle species, *P. egaliksensis* does not produce noticeable scent or nectar. The umbels are few-flowered, bloom more or less in synchrony, and remain in flower for only a few days at most. Thus, among the homostylous taxa, *P. egaliksensis* seems to have the least opportunity for outcrossing. In biogeographic terms, the species is successful with a wide geographic range from Alaska to Greenland, although it is never abundant anywhere in the range.

IV. Biogeographic implications of distyly and homostyly.

Distyly.

The existence of plant taxa that are obligate outcrossers is not unusual in temperate latitudes. Two of the distylous species, *P. alcalina* and *P. specuicola,* do not have boreal distributions and are narrow endemics from Idaho and Utah, respectively. Their restricted ranges may reflect restricted ecological conditions or limited pollinators, or both.

In the arctic and boreal latitudes, however, the presence of obligate outcrossers is less common. Until relatively recently, the concept has been widespread that northern plants are reproductively at the mercy of a stressful climate. They must have the ability to reproduce vegetatively because pollinator dependence is impractical. The work of Kevan (1972) in the Canadian Arctic and Tikhmenev

(1985) on Wrangel Island has shown that arctic plants can indeed be pollinator dependent, and Murray (1987) has discussed fallacies in the belief that plant reproductive strategies are any less complex in the Arctic than in more southern latitudes.

Primula anvilensis, P. borealis, P. cuneifolia subsp. *cuneifolia, P. mistassinica, P. tschuktschorum,* and *P. nutans* are all distylous species growing in Alaska. *Primula nutans* does sometimes reproduce vegetatively by rhizomes, but the other taxa do not. They must therefore be to some extent dependent on pollinators for reproduction. While *P. cuneifolia, P. mistassinica,* and *P. tschuktschorum* are uncommon and have restricted ranges, *P. anvilensis, P. borealis,* and *P. nutans* are relatively abundant. At least by human standards, the environment of the Bering and Chukchi seacoasts is extremely rigorous, and it is noteworthy that on the Seward Peninsula, populations of *P. anvilensis* and *P. borealis* that are virtually sympatric with *P. tschuktschorum* can thrive while the latter species may be endangered. If pollination is a major restricting factor for *P. tschuktschorum,* the other distylous taxa must utilize a more reliable pollinator or a more diverse combination of pollinators than *P. tschuktschorum.* These three species, at least, seem to provide good evidence that while distyly in northern latitudes may be rare, it can be a successful breeding system.

Distylous/homostylous pairs at the diploid level.

The two subspecies of *Primula cuneifolia* and the example of *P. tschuktschorum* support the conventional wisdom that distyly breaks down when pollinators are unreliable. Distylous *P. cuneifolia* subsp. *cuneifolia* inhabits only a small regon in the western Aleutian islands where the notoriously wet and windy climate seems not at all conducive to insect activity, and most of its range is in the climatically more benign Kamtschatka and Khabarovsk regions of the Soviet Union. This area was not extensively glaciated during late Valdai (Wisconsin) glaciations (Velichko 1984). In contrast, *P. cuneifolia* subsp. *saxifragifolia* extends throughout the Aleutian islands and the mountains of Alaska where deglaciation has occurred only in the last 10,000 years. It is likely that selection for reproductive assurance in the pollinator-limiting climate of the Aleutian-Commander Island arc created the autogamous morph subsp. *saxifragifolia* there. This form was then able to spread as the Alaskan glaciers retreated, and is now known from as

far south as Vancouver Island. This wide range throughout recently ice-covered mountain chains indicates a relatively rapid spread of the homostylous morph. An alternative but more awkward explanation is that *P. cuneifolia* subsp. *cuneifolia* had a wide pre-glacial distribution that was reduced to refugial pockets during glacial advances. Parallel selection for autogamy in environments with depleted insect faunas might theoretically create the homostylous morph several times. However, except for the outermost Aleutian Islands closest to the Asiatic coast, there is a complete lack of the distylous form of *P. cuneifolia* in Alaska. This suggests that *P. cuneifolia* subsp. *cuneifolia* is derived entirely from its outcrossed Asiatic relative and is only a recent arrival in North America via the Aleutians and the mountain chains of mainland Alaska.

The example of *Primula tschuktschorum* may represent the effects of biogeographic perturbations as well. This species probably had a wider distribution prior to the Quaternary glaciations. Glacial advances and retreats and concommitant changes in sea level produced considerable climate fluctuations in the Beringian region (Hopkins 1982) and a substantial change in the insect fauna of the Seward Peninsula has been documented (Matthews 1974). It is likely that the reduced status of *P. tschuktschorum* is a result of a depauperate pollinator fauna. There would thus be strong selective pressure for the reproductive assurance of homostyly. It seems appropriate to view *P. eximia* as the product of this selective pressure, wherein the ability to self-fertilize, perhaps combined with substantial amounts of facultative outcrossing to provide some genetic variability has resulted in a flourishing and well-differentiated species without polyploidy or hybridization.

Homostyly and Polyploidy.

While the breakdown of distyly is clearly connected with polyploidy, the reasons for the breakdown have never been explained. Distyly can obviously be maintained at the tetraploid level. As well as the examples given in Table 4.7, all eight species in *Primula* section *Parryi* of western North America are distylous at $2n = 4x = 44$, and Dowrick (1956) showed that distyly is maintained in artificially produced autotetraploids of *Primula obconica*. Therefore, polyploidy per se cannot be the driving factor behind the breakdown of the syndrome. I suggest that the disruption of the S complex with polyploidy is due not to chromosomal or genetic duplication increasing the frequency of crossovers, but rather to the hybridization that tends to

precede higher levels of polyploidy coupled with selection for reproductive assurance via selfing.

Among the polyploid taxa discussed above, tetraploid *P. egaliksensis* is clearly of hybrid origin. The homostylous members of section *Aleuritia* are all 6x or higher, and Stebbins (1950, 1973) believes that almost all successful higher polyploids are allopolyploids. This means that they are the products of some degree of reticulate evolution, with genomes received from different species or perhaps only from different ecotypes within a single species. While the distinction between autopolyploidy and allopolyploidy is somewhat artificial, in a general sense allopolyploids are hybrids. Like any hybrid, they must compete with already successful parental genotypes and often can become established only when appropriate open or "hybrid" habitats are available (Anderson 1948; Stebbins 1985).

In chapter 5 I discuss a probable phylogeny of section *Aleuritia* in North America in relation to Quaternary biogeography. Paleoecological reconstructions of the North American landscape during the past 100,000 years have shown that periodic glacial expansion and retreat influenced distribution of the boreal forest and offered opportunities for separation and recombination of *Primula* gene pools, as well as areas for colonization. The close phenetic resemblance of the members of section *Aleuritia* (Chapter 3) supports the hypothesis that these taxa are part of a reticulate phylogeny, i.e., that they are of allopolyploid origin. The ability to self-fertilize that is concommitant with homostyly was probably the factor that has enabled them to exploit new habitats and survive so sucessfully.

Figure 4.7 shows a hypothetical pathway for homostyly to develop via allopolyploidy. The critical point is that the ability to self-fertilize overcomes the initial reproductive barrier that any newly derived polyploid must face. If polyploidy follows hybridization (and it can, as the famous example of the tetraploid hybrid cultivar*Primula kewensis* demonstrates), any chance homostylous individual would have a great advantage over a distylous individual that faces reproductive problems from intramorph incompatibility, hybridity, and a multiplied chromosome complement. Strong selection would therefore favor homostylous polyploids. Self-fertility plus a diverse genetic background could give homostylous polyploid

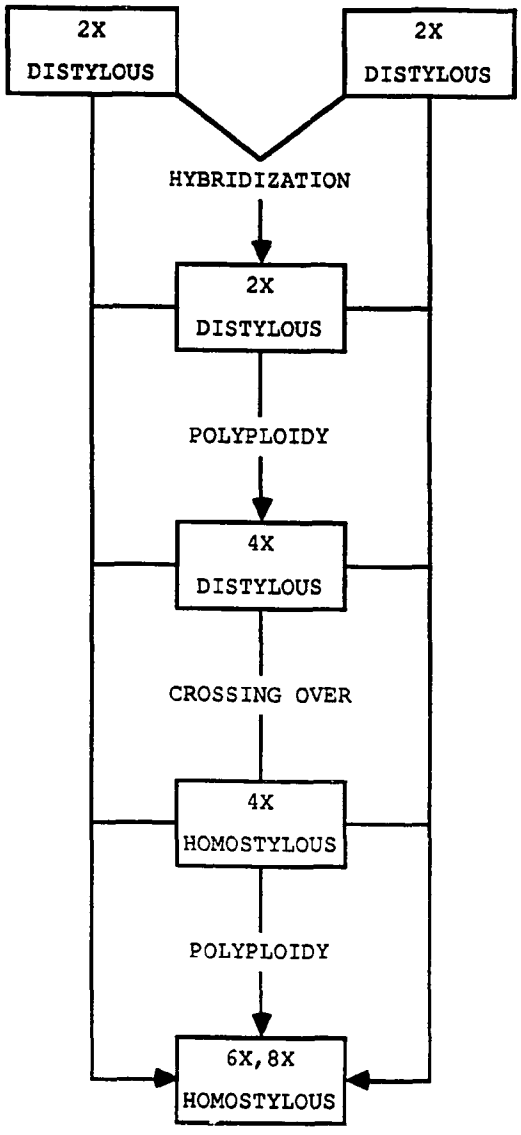


Fig. 4.7. Hypothetical pathway for the development of homostyly and polyploidy.

individuals the ability to become established in different environments from the parental diploids.

Moreover, polyploidy can protect against the detrimental effects of inbreeding by acting as a buffer against fixation of homozygosity. For example, in a diploid, if the original proportion of heterozygotes in a population is 0.5, after one generation of selfing this proportion is reduced by one half. In a tetraploid, however (assuming tetrasomic inheritance), heterozygotes can be simplex (Aaaa), duplex (AAaa), or triplex (AAAa). After one generation of selfing, the proportion of heterozygotes would still be reduced, but by a much smaller amount. Even low levels of outcrossing can maintain a degree of heterozygosity in generally autogamous species (Richards 1986), and as described previously, most of the homostylous polyploid Primulas in North America retain features that promote outcrossing.

There is some evidence for genetic diversity in the higher polyploid taxa of section *Aleuritia*. In an isozyme analysis of the hexaploid species *P. scotica*, Piper (unpublished mss.) found multiple banding patterns in three out of twelve loci that were to him indicative of fixed heterozygosity through allopolyploidy. In Europe, the biogeographic story of glacial expansion and retreat and the patterns of diploidy and polyploidy closely parallel those seen in North America. *P. scotica* is the European equivalent of *P. incana*, and the results of Piper's study provide the first empirical evidence for an evolutionary scenario that may have been repeated on both continents.

These European and North American examples suggest that polyploidy and hybridization can act in conjunction with selection for autofertility to create successful homostylous taxa. The establishment of randomly occurring polyploid or hybrid individuals would be promoted by homostyly because it confers the ability to self-fertilize. The existence of several tetraploid distylous taxa shows that the S complex can be maintained through at least low levels of polyploidy. Further systematic analyses are needed to examine the background of these species. I suggest a reasonable hypothesis is that they are autopolyploids, or at least represent the conjugation of only slightly different parental genomes. As such, they would have only the barrier of chromosome number to overcome and would be more likely to be able to backcross with parental taxa. The more diverse the genome of a polyploid, i.e., the stronger the degree of allopolyploidy, the more difficult parental

backcrosses become, and the more likely it is that self-fertility via homostyly is required for success.

V. Summary.

A number of conclusions can be reached from this survey of distyly and homostyly in four sections of the genus *Primula* in North America.

Taxonomy. Distyly and homostyly can have strong taxonomic implications in the genus. They can themselves be used as a character of variable weight, or they can be important because they dictate the predominant breeding system, and breeding systems often have morphological correlates. In a morphologically conservative genus like *Primula*, attributes such as flower size and pedicel length can be key taxonomic markers. Homostylous primulas generally support the trend of smaller flowers and more compact inflorescences seen in other autogamous taxa. However, there are notable exceptions and several homostylous taxa show features indicative of at least facultative outcrossing.

Distribution. In the northern Primulas there are examples of distylous species at the diploid and tetraploid levels, distylous/homostylous pairs at the diploid level, and homostylous higher polyploids. There is evidence that homostyly is strongly associated with hybridization, most often in the form of allopolyploidy.

Biogeography and reproductive assurance. Distributions of homostylous and distylous species of *Primula* indicate that distyly and obligate outcrossing can be an effective reproductive strategy in the Arctic for certain taxa. However, the examples of distylous/homostylous pairs suggest that homostyly may be more successful in certain circumstances. As expected, homostylous taxa are particularly effective in colonizing recently deglaciated areas. It appears that reproductive assurance is a prime factor responsible for the establishment of homostylous taxa in northern regions. This may be due to direct selection when climatic perturbations disrupt pollinator efficiency or when taxa migrate beyond the range of reliable pollinators, or it may follow selection for autogamy when reproductive isolation is the result of hybridization and/or polyploidy.

Chapter Five

Evolution of the genus *Primula* in North America: a cladistic and biogeographic analysis.

I. Introduction

In North America there are twenty one species of *Primula* representing five sections of the genus. No phylogenetic or biogeographic analysis of these species has ever been done. With a thorough taxonomic analysis now complete for most of the North American species (Chapter 2), it is possible for the first time to understand the biogeographic patterns of the genus in this region and to undertake some limited phylogenetic reconstructions. These reconstructions require two separate perspectives. The first is an understanding of the present day taxonomy and biogeography of closely related species (or lower taxa) in Asia and northern Europe. Unfortunately, this understanding is not fully available due to the number of taxonomic problems remaining, particularly with the Asiatic species in the genus. The second perspective needed is an historical one. Contemporary floristic patterns in arctic and boreal North America are the product of both present day processes and environments and processes of the past. While our view of the past must always be through a glass darkly, modern techniques in palynolgy, archeology, climatology, and glaciology have made it possible to reconstruct many aspects of the ancient landscapes of North America. In particular, the last 20,000 years have been subjected to considerable scrutiny and we now know much about what changes have occurred in the landscape, and how and where the biota has responded to advances and retreats of the glacial ice and concurrent climatic changes.

In this chapter I first present a brief summary of late Quaternary environments in North America, the North Pacific, and Europe. This summary is based on syntheses presented by a number of authors, notably Wright and Frey (1965), Hopkins (1967; 1983), Matthews (1979), Wright (1983), Ritchie (1984), and Hamilton et al. (1985), for North America, and Flint (1971), Nilsson (1983), Tsukada (1983; 1985) and Velichko (1984) for Europe and Asia. I then examine present day distribution patterns of the sections of *Primula* in North America and explain these patterns in relation to both historical and contemporary environments.

Finally, I present cladistic analyses for each of the four arctic/boreal sectionsof the genus, and discuss the contributions of this method of phylogenetic reconstruction and its relationship to descriptive biogeography.

II. Quaternary environments.

North America.

Due to the length of time involved, reconstructions of the details of late Tertiary and early Quaternary environments are difficult. We know that floristic patterns across the entire globe were probably considerably different than those of today, and there has been much speculation about when contemporary vegetation associations originated. It is suggested that a vegetation type generically similar to the modern boreal forest was in place across the Holaractic by the late Tertiary, and that patches of tundra may also have been present at that early date (Ritchie 1984). However, climatic and geological events of the Quaternary Period, the last 1.6 million years, are perhaps the most significant determinants of contempary biotic patterns.

The Quaternary was composed of intervals of global climatic fluctuations, glacial advances and retreats, sea level changes, and emergence and submergence of low-lying land masses. This pattern was continually repeated at different time scales throughout the entire Pleistocene but the details are clearest for the most recent glacial episode, the Wisconsinan. The term "Wisconsin glaciation" includes both glacial advances and retreats during the time period 100,000 to 10,000 BP, and is traditionally divided into Early (100,000-55,000 BP), Middle (55,000-23,000 BP), and Late (23,000-10,000 BP). Ice cover was greatest on this continent during the Late Wisconsin, ca 18,000 BP (Wright and Frey 1965; Flint 1971). After this, climatic changes brought glacial shrinkage and eventual retreat to the few remaining ice caps of today. Extensive palynological work has made it possible to reconstruct vegetation response to climatic change and glacial advances and retreats. Figures 5.1 and 5.2 show modern vegetation of North America and current interpretations of vegetation and glacial limits at the height of the last glaciation, respectively.

There are several key points on these maps relevant to a discussion of the modern biota. First, much of interior Alaska and the Yukon remained unglaciated during the late Wisconsin and this area was joined to Siberia via an extensive land

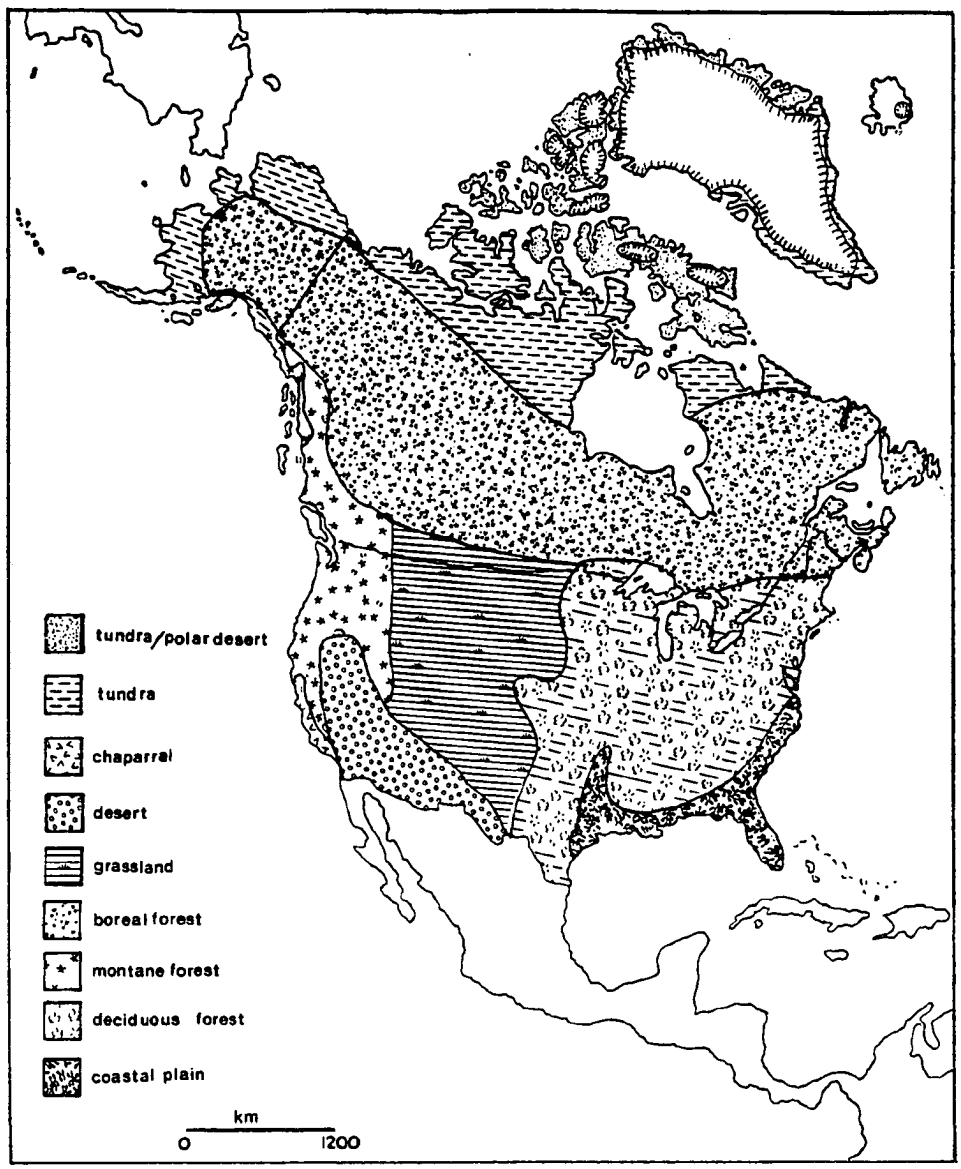


Fig. 5.1. Modern vegetation patterns in North America (after Cain 1944).

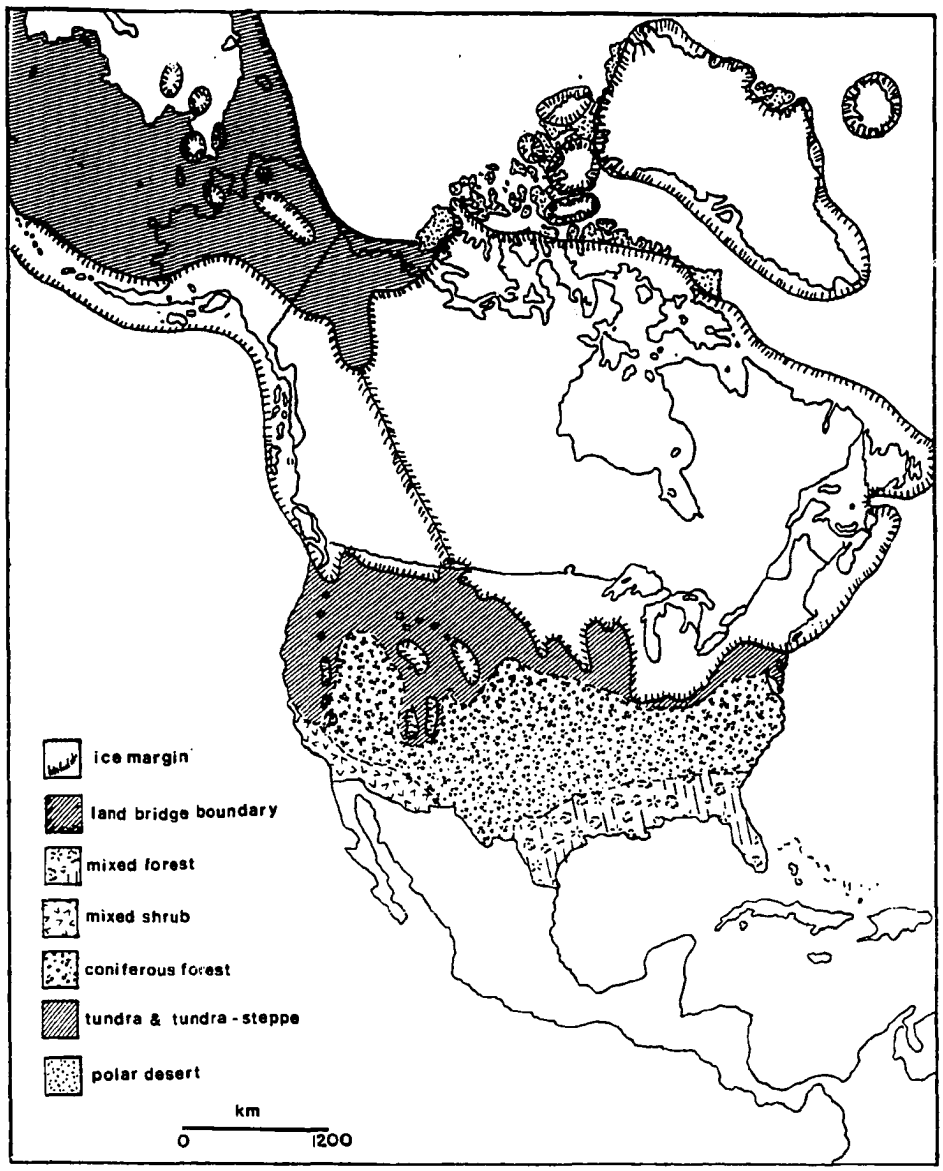


Fig. 5.2. Generalized vegetation patterns in North America ca 18,000 years BP. (after Flint 1971, Murray 1987, and Wright, 1983).

bridge across the Bering Strait. The details and significance of this region known as Beringia has been been discussed in detail by Hultén (1937) and Hopkins (1967; 1983). Second, most of Canada was covered by an extensive ice sheet, although several unglaciated areas may or may not have acted as biological refugia (see, among others, Savile 1961; Packer 1969; Ives 1974; Packer and Vitt 1974; Brassard 1971). Third, the expanse of coniferous forest extended much further south than in the present day, across the continent to areas that are now grasslands or desert.

When climatic change and glacial retreat began after 18,000 years BP, the zone of boreal forest moved north and east. Similarly, the tundra zone moved latitudinally north and altitudinally up into previously ice-covered areas (Wright 1983). The Bering Land Bridge was submerged, and the North American-Siberian connection severed for the last time by about 15,000 years BP (Hopkins 1983).

Europe

In Europe there was a very similar pattern of multiple glaciations during the Quaternary Period. There the Weischel glaciation was more or less synchronous with the North American Wisconsin glacial episodes. When Laurentide ice was at its maximum extent, continental ice sheets covered most of Britain, Scandinavia, and the islands in the Arctic Ocean, with extensive mountain glaciation in the Alps, Pyrenees, Carpathians, Apennines, and mountains of the Balkan Peninsula (Flint 1971; Nilsson 1983). There has been considerable debate about what regions in Europe were not ice-covered and might therefore have served as biological refugia. Among those suggested are coastal nunataks in Norway, the Lofoten Islands, and much of southern Britain (Flint 1971).

Even if there were unglaciated areas close to or within the ice margins, they must have been rather severe environments. Large expanses of tundra and polar desert lay between the Alps and the Scandinavian ice sheet, and the treeless region stretched as far south as the Iberian Peninsula. This tundra zone graded into coniferous forest in the south and steppe in the east.

The North Pacific

The continental ice sheets of Europe did not extend beyond western Siberia. In the Far East, there was local alpine glaciation in Chukotka, along the Bering Sea Coast and Sea of Okhotsk, and the Aleutian islands were almost completely covered by glaciers (Velichko 1984; Hamilton et al. 1985). In Kamtschatka, alpine glaciers were present at the higher elevations but apparently did not reach sea level. In Japan

there was only limited alpine glaciation, in the Japanese Alps of central Honshu and on the Hidaka mountains of southeastern Hokkaido (Tsukada 1983).The modern vegetation of the North Pacific Bering Arc is composed of a mixture of tundra (the higher peaks of northern Japan, Kamtschatka, and the Commander-Aleutian Islands), lowland meadows (Kamtschatka and the Commander-Aleutian Islands), *Pioea-Abies* or *Pinus* conifer forest (Sakhalin, Kurile Islands, Hokkaido and subalpine Honshu), and mixed conifer and temperate deciduous forest (Sea of Okhotsk). In contrast, palynological studies indicate that at the height of the last glaciation, coniferous forest lay from Hokkaido south throughout the Japanese archipelago. The vegetation from northern Hokkaido up to the alpine glaciers in Kamtschatka was primarily tundra with some birch-larch deciduous forest along the Sea of Okhotsk. As glaciers retreated, formerly ice-covered areas became alpine tundra or the lowland meadows we see in the Aleutian Islands today, and the coniferous forest became restricted to subalpine elevations when it was replaced in the lowlands by temperate or, in southern Japan, tropical deciduous species (Tsukada 1985).

III. Phylogenetic reconstruction of *Primula* in North America: biogeographic and cladistic analysis.

The current trend in systematics is to use cladistic methods with detailed character analysis to estimate a phylogeny. These methods have a number of variations (see, for example, Wiley 1981; Platnick and Funk 1983; Duncan and Steussy 1984), but there are restrictions common to all. It is generally agreed that cladistic methods are most instructive when polarities of character states (ancestral versus derived) can be determined, when there are a number of characters to compare, and when reticulation (i.e. hybridization) is not extensively involved in the phylogeny. Consequently, cladistics are easiest to apply at higher taxonomic levels such as families or genera, or within a taxon like a section of a genus, when most of the members are known and can be included within the analysis.

The genus *Primula* is not an easy candidate for cladistic analysis below the sectional level. It is large (ca 500 species), and very little of it has been reviewed in a contemporary systematic treatment. It is a morphologically conservative genus, where both species and sections are often delineated only by a suite of overlapping characters. Character states are unclear in a number of taxa, polarities can only be

assigned to a few with confidence, and there are not many diagnostic unrooted characters with which to work. Furthermore, in at least section *Aleuritia,* it is clear that hybridization via allopolyploidy has been a major factor in the diversification of the group.

For these reasons, cladistic analyses of *Primula* at the species level must be limited. Here only small and sometimes admittedly incomplete groups are analyzed. They correspond to sections, or parts of sections, of the genus which are clear phenetic groups (Chapter 3) and which are recognized in current taxonomic treatments. Section *Cuneifolia,* which contains only three species is treated in its entirety. In section *Crystallophlomis,* only the four species found in northeastern Siberia and northwestern North America are examined. Biogeographic and morphological evidence suggests that they are the most closely related taxa in this section. In section *Aleuritia,* only the four diploid species in North America are subjected to cladistic analysis. Other species, which are allopolyploids, are added to the cladogram on the basis of other evidence which is discussed in the text.

These analyses were performed using a mixed method parsimony algorithm on the MIX routine of the package PHYLIP (Felsenstein 1984) and drawn with the program MacClade (v. 2.1, by W. Maddison and D. Maddison, Harvard University) and MacPaint (v. 1.4, by D. Atkinson, Apple Computers, Inc.). PHYLIP calculates the tree with a minimum number of evolutionary changes, allowing user-assigned assumptions for each character. In the Camin-Sokal method (Camin and Sokal 1965) it is assumed that ancestral states are known, and a unidirectional character state change is the most likely. Under the Wagner method (Kluge and Farris 1969) ancestral states may or may not be known, but character state changes in any direction are equally likely.

Where possible, polarities were assigned. Distyly and diploidy were always defined as plesiomorphies, with homostyly and polyploidy the respective apomorphies. White flower color is treated as an apomorphy on the basis of its rarity in the genus. I suspect that it is often a homoplasy, i.e., a derived character that has originated independently several times. Other morphological characters were polarized using other sections and/or related species as the outgroup. Geographic distribution in North America was designated apomorphic because in *Primula* the overwhelming number of species are found in Asia. While it has been argued for some taxa that the center of diversity does not necessarily have to be the center of

origin (Cain 1944), the Asiatic origin of *Primula* has never been in question (Wendelbo 1961; Valentine 1962). For other characters, it was not possible to determine which state was advanced and these characters were left unpolarized.

A. Section *Cuneifolia* Balfour.

Biogeography. This small section contains only three species, one of which, the type species, has a number of infraspecific taxa. Two of the members, *P. cuneifolia* Ledeb. and *P. suffrutescens* Gray, are found in North America. The overall distribution of section *Cuneifolia* is the Pacific Basin: northern Japan, the Kurile Islands, Kamtschatka, and the Commander-Aleutian chain, through the mountains of Alaska. *P. suffrutescens* is isolated in the high mountains of the Sierra Nevada (Fig. 5.3).

On the basis of the paleoecological reconstruction of the North Pacific and North America during the Quaternary, I suggest the following biogeographic setting for the evolution of this group of taxa. The Japanese subspecies of *P. cuneifolia* are most likely products of the late Wisconsin glaciation, when the range of *P. cuneifolia* or its ancestral stock was larger and reached further south than at present. Populations were isolated in pockets of alpine tundra on the mountain peaks of Honshu as the tundra and coniferous forest moved north, and today are only minor geographic variants of the more widespread subspecies *cuneifolia*.. Subspecies *saxifragifolia* is a North American homostylous derivative of fairly recent origin in the Aleutian-Commander island chain during the early stages of deglaciation through selective pressure for self-fertility (Chapter 4) in an environment where pollinators were unreliable. Once established, this ability to self enabled it to spread rapidly throughout Alaska and down the coastal mountains during the next 10,000 years, whereas the distylous subspecies *heterodonta* and *hakusanensis* remain as narrow alpine endemics, restricted both by lack of appropriate tundra habitat or their obligatory outcrossing. The low-level morphological differentiation of the four subspecies is evidence that they may have diverged only recently. Without detailed taxonomic and genetic analysis, it is impossible to give a relative date of divergence of the well-marked species *P. nipponica*. It may also be of Pleistocene origin, either isolated longer from earlier glacial episodes, or simply subjected to stronger selective forces. The tetraploid, but still distylous *P. suffrutescens*, may be a relatively young isolate, but it is also possible that it is derived from the remnants of

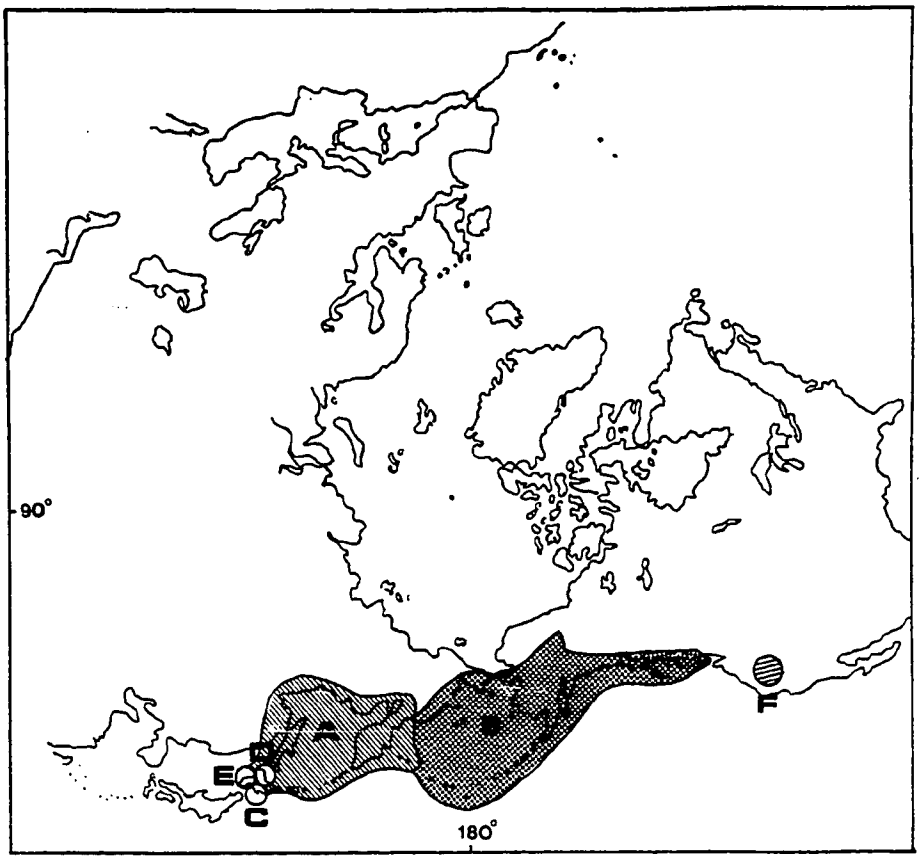


Fig. 5.3. Distribution of *Primula* section *Cuneifolia*. A. *P. cuneifolia* subsp. *cuneifolia*. B. *P. cuneifolia* subsp. *saxifragifolia*. C. *P. cuneifolia* subsp. *heterodonta*. D. *P. cuneifolia* subsp. *hakusanensis*. E. *P. nipponica*. F. *P. suffrutescens*.

an older more extensive distribution of *P. cuneifolia* or an extinct ancestor. This species appears to link section *Cuneifolia* with section *Parryi* of the western cordillera in North America. The latter section is composed of eight distylous tetraploids which, like the members of section *Cuneifolia*, have a base number of 11 and involute vernation of the leaves. Detailed taxonomic analysis is needed before its position in the genus can be determined.

Cladistics. Analysis was done on all the taxa in section *Cuneifolia* , including the subspecies of *P. cuneifolia*. Character states and polarities are given in Table 5.1.

Table 5.1. Character states for the species in *Primula* sect. *Cuneifolia*. * indicates an ancestral state. Multistate characters are ordered in the order given.

1. Flowers rose-pink (0*) white (1)
2. Ploidy level 2x (0*) 4x (1)
3. Plants caespitose (0*) rhizomatous (1)
4. Flowers > 10 mm in width (0) < 10 mm in width (1)
5. Lobes emarginate (0*) deeply bifid (1)
6. Species found only in Asia (0*) N. America and Asia (1) N.America only (2) (0-1-2)
7. Flowers distylous (0*) homostylous (1)
8. Leaves evenly toothed (0) unevenly toothed (1)
9. Teeth large and obtuse (0) small and acute (1)
10. Main range in Asia (00*) Asia and N. America (01) N. America (2) (0-1-2)

P. nipponica	1	0	0	1	0	0	0	0	0	0
P. suffrutescens	0	1	1	0	0	2	0	0	0	0
P. cuneifolia	0	0	0	0	0	1	0	0	0	1
subsp. *saxifragifolia*	0	0	0	0	0	1	1	0	0	2
subsp. *hakusanensis*	0	0	0	0	0	1	0	0	1	0
subsp. *heterodonta*	0	0	0	0	0	1	0	1	0	0

This results in the cladogram given in Fig. 5.4.

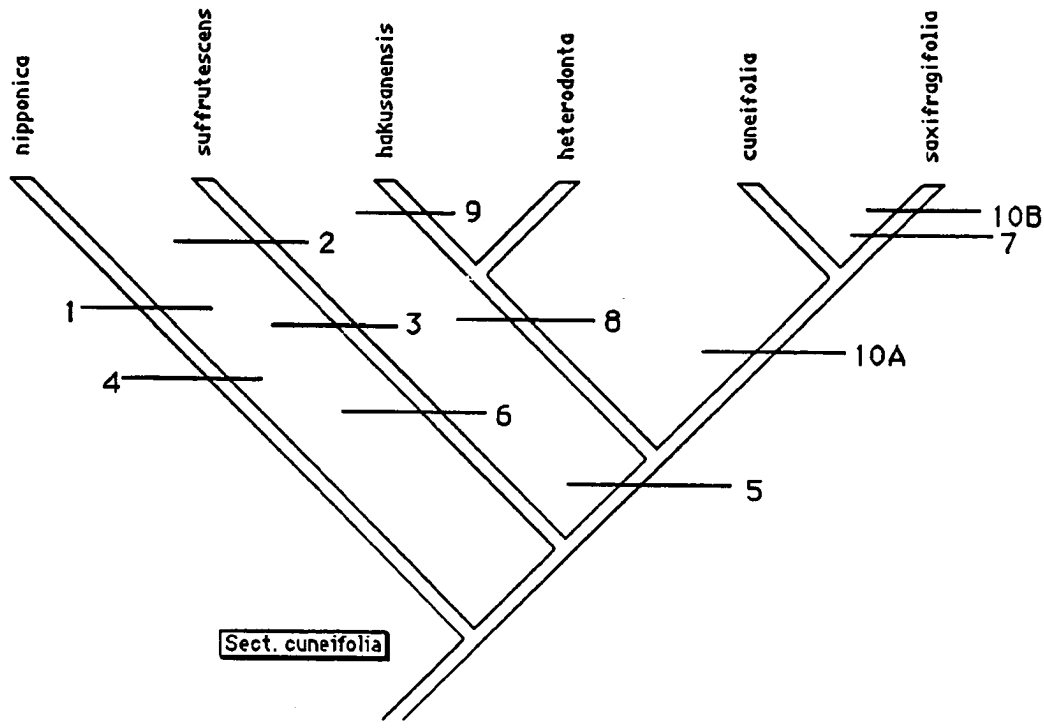


Fig. 5.4. Cladogram of sect. Cuneifolia. Letters represent alternative character states of a multistate character.

This cladogram agrees with the biogeographic evidence for this section. The separation of the subspecies of *P. cuneifolia* (*hakusanensis, heterodonta, cuneifolia and saxifragifolia)* are represented here, following cladistic theory, as bifurcations. If the biogeographic story I have presented is credible, multifurcations may be a more accurate representation of the evolution of these taxa. It does not seem unreasonable that range fragmentation into a number of isolated populations could have occurred in this group of taxa and in other northern ones as well. For example, a taxon with a wide range could be disrupted by the growth of glaciers in intervening mountain ranges and, given sufficient time and ecological or reproductive restrictions, the isolated populations could become the geographic entitities we see today.

B. Section *Crystallophlomis* Ruprecht.

Biogeography. Most of the species in this large section are found in the Himalayan mountains of Asia. In eastern Siberia and northwestern North America there are four species (Fig. 5.5): *Primula nivalis* Pallas, *P. xanthobasis* Federov, *P. tschuktschorum* Kjellman, and *P. eximia* Greene. *P. eximia* has been treated as a part of *P. tschuktschorum* s. lat., but I have presented the case for considering it a separate species, the homostylous derivative of *P. tschuktschorum*, elsewhere (Kelso 1987b).

The paleoecology of the Bering Strait region suggests that *P. tschuktschorum* and *P. xanthobasis* diverged early from the ancestral *P. nivalis* stock, perhaps by the late Tertiary or when Pleistocene glaciations isolated populations in the mountains of Chukotka and eastern Siberia. It is likely that *P. tschuktschorum* was once widespread at least in central Beringia, and that its current endemism around the Bering Strait is the result of late Pleistocene events. I have suggested earlier (Chapter 4) that because *P. tschuktschorum* is distylous and therefore an obligate outcrosser, it has suffered from an impoverished insect fauna, and populations may be reaching critically low numbers due to inadequate pollination. *P. eximia* is treated as a recent homostylous derivative that developed, like its counterpart *P. cuneifolia* subsp. *saxifragifolia*, from strong selective pressures for self-fertility acting on a chance mutation to homostyly. *P. eximia* is thriving in the Bering Strait region and has been able to migrate via the mountain chains of Alaska and the northeast Asiatic coast. Because they theoretically do not need to attract pollinators,

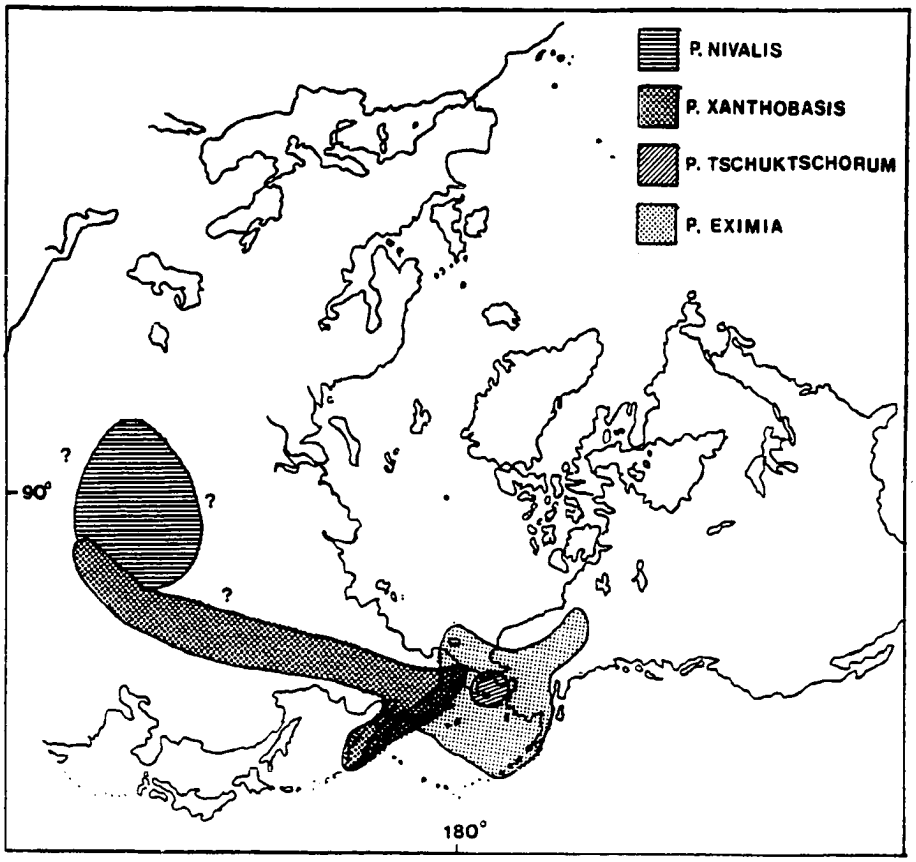


Fig. 5.5. Distribution of northeastern Asiatic and North American members of *Primula* sect. *Crystallophlomis*.

homostylous taxa are expected to be less showy versions of their distylous and outcrossing parent (Chapter 4). *Primula eximia* is a somewhat unusual homostyle because it is larger, more robust, and has more flowers than its putative distylous parent *P. tschuktschorum*. On the basis of these characters, it resembles *P. nivalis* even if other aspects of morphology, ecology, and biogeography ally it to *P. tschuktschorum*.

Cladistics. Because of their overall morphological resemblance and their biogeographic affinities, I have treated *P. nivalis, P. xanthobasis, P. tschuktschorum,* and *P. eximia* as a phylogenetic branch of section *Crystallophlomis* and subjected only these species to a cladistic analysis. The confused taxonomy of the other members of the section precludes using them in the analysis, so this discussion will focus on an admittedly incomplete group. Table 5.2 gives character states for the four taxa.

Table 5.2. Character states for the Siberian-North American members of sect. *Crystallophlomis*. * indicates ancestral state.

1. Farina white (0) yellow (1) none (2) (unordered)
2. Flowers distylous (0*) homostylous (1)
3. Flowers many (0) few (1)
4. Leaf margins mostly entire (0) serrate (1)
5. Range mostly in Asia (0*) mostly in N. America (1)

P. nivalis	0	0	0	1	0
P. xanthobasis	1	0	0	1	0
P. tschuktschorum	2	0	1	0	1
P. eximia	0	1	0	0	1

This results in the cladogram shown in Fig. 5.6.

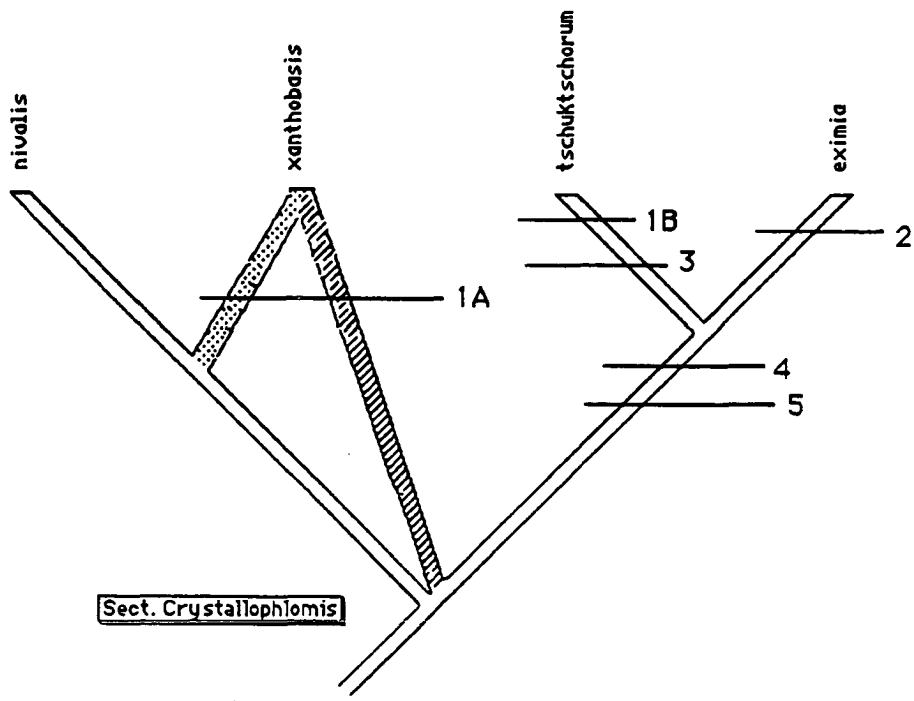


Fig. 5.6. Cladogram of sect. Crystallophlomis (Beringian species). Letters represent alternative character states of a multistate character. Shaded branches represent alternative placements.

Two alternative representations for the position of *P. xanthobasis* are shown by the shaded branches. One is a trifurcation between *P. nivalis, P. xanthobasis,* and the *eximia-tschuktschorum* branch, and the other suggests a closer relationship to *P. nivalis* than to *P. eximia -tschuktschorum*. Both possibilities seem equally likely in biogeographic terms. If the ancestral *P. nivalis* stock was widespread and then split up by events of the Pleistocene, *P. xanthobasis* and *P. tschuktschorum* could be of more or less equal age and therefore be considered a phylogenetic trifurcation. Alternatively, *P. xanthobasis* may be a segregate of *P. nivalis*. The two species have adjacent ranges, and morphologically they differ only in their farina color and number of flowers, characters for which the genetic basis is not clear. It is perhaps sufficient to conclude only that these four representatives of sect. *Crystallophlomis* are close relatives representing different responses to Pleistocene events in Beringia.

C. Section *Aleuritia* Duby.

Biogeography. This section is one of the largest in the genus. Found across North America, Europe and Asia, it is characterized by a high degree of polyploidy with levels of 2x, 4x, 6x, 8x, and 14x. Taxa with the higher chromosome numbers are all homostylous, whereas diploids and tetraploids are usually distylous (Chapter 4). In North America, section *Aleuritia* is represented by four diploid species (Fig. 5.7) and four polyploid species ranging from 4x to 14x (Fig. 5.8).

I believe that the diversification of section *Aleuritia* in North America can be explained by classical models of allopatric speciation in combination with extensive hybridization and polyploidy. Stebbins (1984, 1985) has provided a theoretical evolutionary framework that explains how a "polyploid pillar" (Stebbins 1950) might develop. In his secondary contact theory, an initially widespread species is fragmented into separate gene pools by ecological or geological events (e.g. glaciation). Over time, these gene pools differentiate, but not enough for complete reproductive isolation. If the ecological or geological barriers are removed (e.g. glaciers retreat and populations migrate), the taxa come into secondary contact with each other and form allopolyploids. Repeated separation and contact can result in backcrosses and a complex pattern of hybrids. The availability of open habitats from whatever perturbations separated the refugial populations gives the new polyploids the opportunity to become established, and sucess is promoted if the

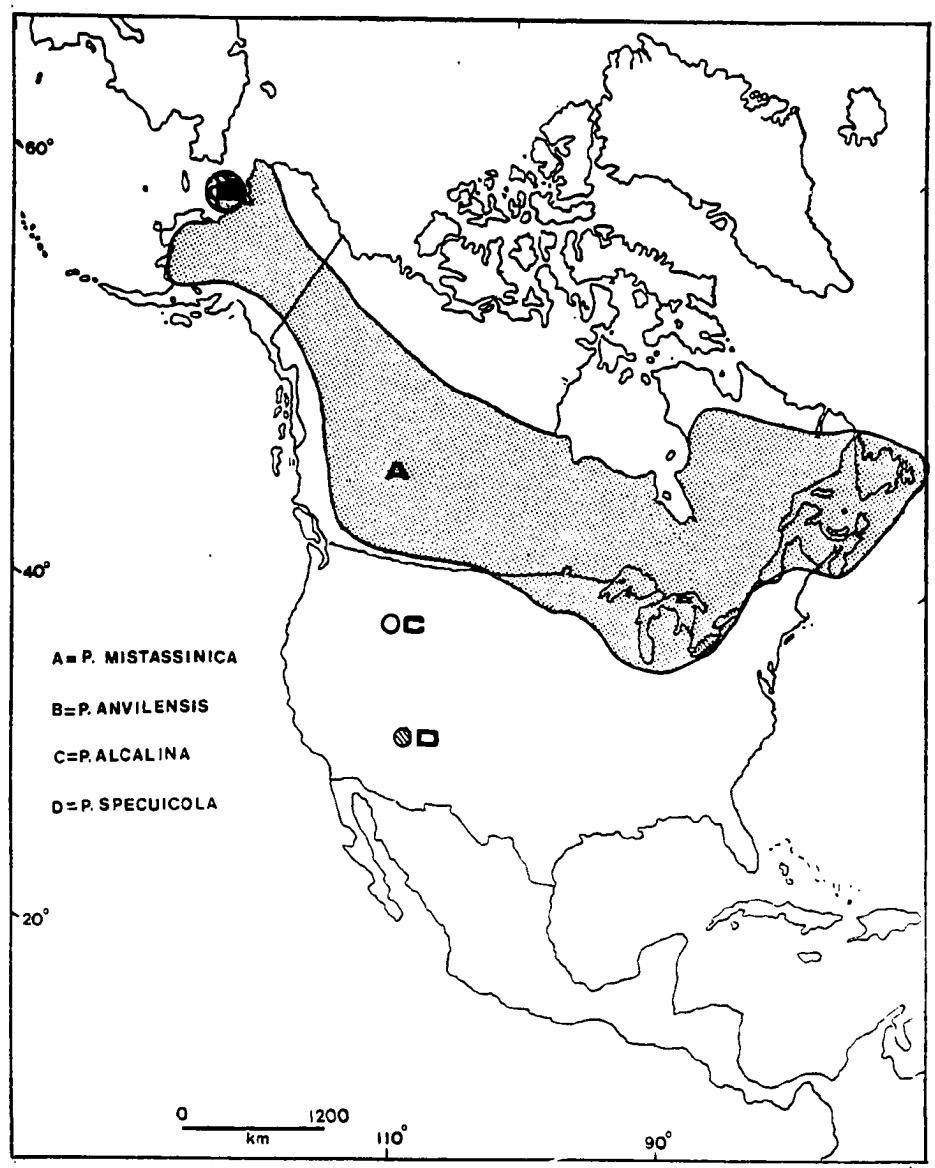


Fig. 5.7. Distribution of diploid species in *Primula* section *Aleuritia* in North America.

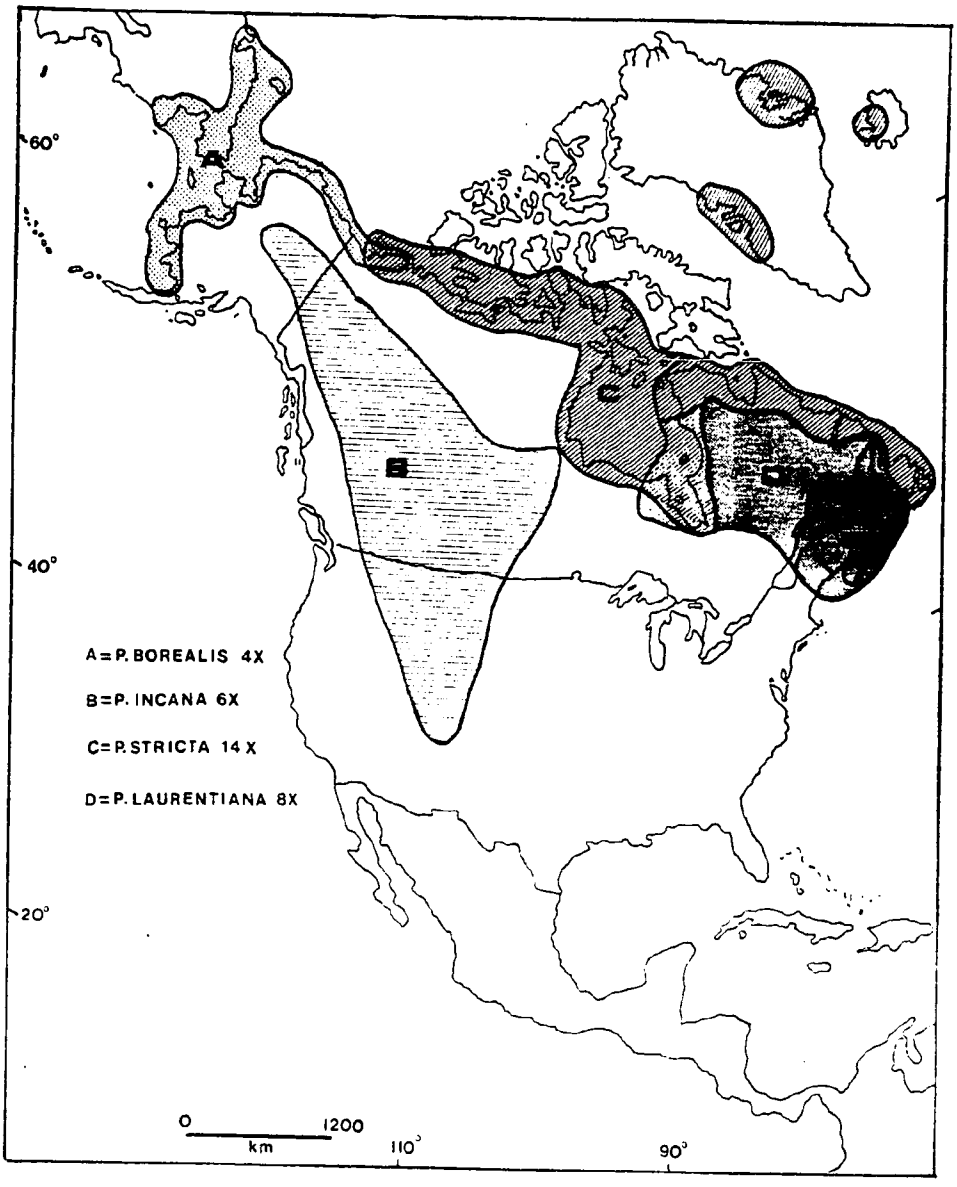


Fig. 5.8. Distribution of polyploid species in *Primula* section *Aleuritia* in North America.

polyploids can self-fertilize. Section *Aleuritia* provides a concrete example for the theoretical framework presented by Stebbins. I offer the following explanation for the diversification of this section in North America.

At least prior to the late Wisconsin glaciation, and perhaps earlier, a taxon similar to *P. mistassinica* was widespread across North America in the boreal regions, including Alaska. Ecologically this proto-*P. mistassinica* was a calciphile, and like the extant taxon, its habitat was in cool, moist sites with low-competition. It was not necessarily a forest (i.e. understory) species, although its general distribution followed that of the boreal forest of the time, loosely defined as a *Picea-Abies* association. With the spread of the glaciers, the boreal forest moved south of its present location and eventually reached across the continent from the southwest to the Appalachians. At this time Alaska was essentially cut off from the rest of North America by the confluence or near confluence of the Cordilleran and Laurentide ice, and a remnant of the proto-*P. mistassinica* remained there to survive on the Seward Peninsula where there is abundant low elevation calcareous bedrock. That remnant is the *P. anvilensis* of today.

South of the ice sheets, there was further fragmentation of the range of the transboreal proto-*P. mistassinica*. The extensive infraspecific variation in the modern *P. mistassinica* led Vogelmann (1956) to suggest glacial survival in several refugia, including Newfoundland, the Appalachians, and the Midwest. This partial differentiation of the gene pool is seen today in the yellow-farinose subsp. *intercedens*, and the small white-flowered Newfoundland morph. I further suggest that, like *P. anvilensis* in Alaska, *P. specuicola* in the southwest and *P. alcalina* in Idaho were isolated from the main range, and adapted in situ to local conditions, rather spectacularly so in the case of the canyon-dwelling *P. specuicola*. In contrast, the eastern refugial populations of *P. mistassinica* did not differentiate at the species level because they were able to rejoin when the boreal taxa migrated north as glacial ice retreated.

Today *P. mistassinica* has a transboreal distribution. It is most abundant in the east, and becomes progressively more rare in Northwest Canada and Alaska. These scattered populations are often along rivers and in areas that were subjected to alpine glaciation in the Late Wisconsin, and are probably the result of post-Pleistocene dispersal. *P. mistassinica* is distylous and self-incompatible, and thus would not appear to be an efficient colonizing species. However, it clearly has been able to

migrate considerable distances.

The divergence and speciation of *P. anvilensis*, *P. alcalina*, and *P. specuicola* were not necessarily contemporaneous or even all from the Late Wisconsin. We know only that conditions during the last glaciation were such that migration and isolation occurred, and speciation was possible. However, without a measure of evolutionary rates, we cannot know whether these processes could have all occurred in the last 20,000 years, or whether the divergence of the diploid relatives of *P. mistassinica* has taken place over a much longer period of time.

Whenever the fragmentation of the diploid ancestral stock occurred, the concatenation of eastern populations provided the impetus for the establishment of the polyploid complex we see today. The hexaploid *P. incana* of the western prairies and the octoploid *P. laurentiana* of eastern Canada are most likely the results of allopolyploidy between the partially differentiated diploid gene pools. These polyploids were able to become established and then spread due to their homostyly and concommitant self-fertility. This homostyly was probably a chance mutation favored by strong selective pressures (Chapter 4).

In Europe, there is a parallel situation with the widespread diploid *P. farinosa*, which also has a large amount of infraspecific variation, and the homostylous polyploids *P. scotica* (6x, northern Scotland) and *P. scandinavica* (8x, Scandinavia). Like *P.mistassinica* in North America, *P.farinosa* probably survived Pleistocene glaciation in several refugia and populations rejoined to form the higher polyploids and infraspecific taxa seen today. North America and Europe share one polyploid species, the decatetraploid *P. stricta*. Knaben (1982) suggested this was a hybrid between *P. scotica* and *P. scandinavica* that spread in postglacial time to North America. I believe that equally likely parents are the North American species *P. incana* and *P. laurentiana*.. *P. stricta* shows a resemblance to both *P. incana* and to *P. scandinavica*, so on phenetic grounds either set of parents could be argued. The contemporary distribution of *P. stricta* is not convincing evidence for either eastward or westward postglacial migration. Its range is larger in North America than in Europe, but not extensively so, and this may only be due to a greater amount of available habitat in the saline and floristically depauperate Canadian Arctic Archipelago. The heritage of *P. stricta* must remain an open question until further genetic evidence for its parentage can be obtained.

The origin of the tetraploid species *P. borealis* of the Bering Sea coast is

somewhat problematic as well. In the past *P. borealis* has been confused with *P. anvilensis* and with *P. mistassinica* but I believe it has an even closer affinity with a Japanese relative of *P. farinosa* L., *P. modesta* Bisset & Moore. *P. modesta* has several infraspecific taxa, including var. *faurei* (Franchet)Takeda and var. *matsumurae* (Petitm.)Takeda. With the exception of its diploid chromosome number and yellow farina, *P. modesta* var. *matsumurae* is almost indistinguishable from *P. borealis*, and there has been confusion of the two taxa in the literature (q.v. *P. borealis*, Chapter 2). A thorough analysis of the taxonomy of the East Asian members of section *Aleuritia* is needed, but I believe that it is reasonable to suggest the halophyte Beringian species *P. borealis* is a late Quaternary tetraploid derivative of the Asian *P. farinosa-P. modesta* stock rather than part of the North American *P. mistassinica* polyploid pillar.

Cladistics. Because the pattern of polyploidy in section *Aleuritia* is a good indication that reticulate evolution has occurred, and because the taxonomy of the Asiatic members remains problematical, a cladistic analysis was done only on the diploid representatives of the section in North America. Table 5.3 show character states for the species used in the analysis, and Figs. 5.9a and 5.9b are the resulting cladograms.

Table 5.3. Character states for diploid species of sect. *Aleuritia* in North America. * indicates an ancestral state.

1. Flower color lilac (0) white (1)
2. Plants farinose (0*) efarinose (1)
3. Habitat calcareous meadow (0) canyon (1)
4. Mean no. of flowers > 8 (0) < 8 (1)
5. Pedicels capillary (0) erect (1)
6. Leaves denticulate (0) serrate (1)

P. alcalina	1	1	0	0	1	0
P. anvilensis	1	1	0	1	0	0
P. specuicola	0	0	1	0	0	1
P. mistassinica	0	1	0	1	0	0

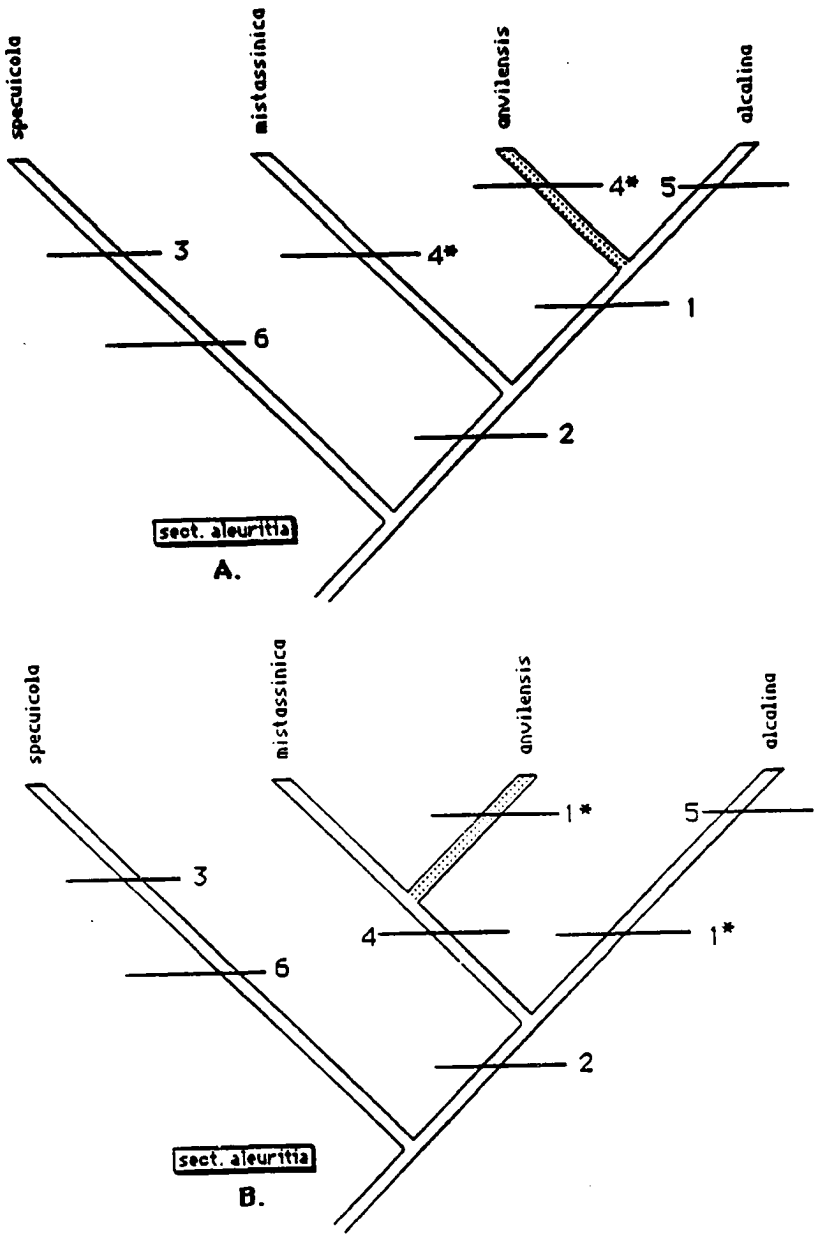


Fig. 5.9. Cladogram of sect. Aleuritia * represents character that originates twice. Shaded branch represents alternative placement.

Both cladograms are equally parsimonious (7 steps). Fig. 5.9a suggests that low flower number develops independently twice, and Fig. 5.9b suggests that white corolla color originates twice. Because the general habit, ecology, and biogeography of *P. anvilensis* ally it closely to *P. mistassinica*, I believe that Fig. 5.9b is the more accurate representation of the relationship between these species.

This analysis was based on attributes of *P. mistassinica* subsp. *mistassinica*, the most widespread of the intraspecific taxa in that species. However, *P. mistassinica* is highly polymorphic. If range fragmentation can be accepted as the ultimate cause of this differentiation, the complete diploid phylogeny of section *Aleuritia* might be most accurately represented by multi-branched forks. The polyploid members of the section, as probable hybrids, must be added as reticulations.

All the North American members of the section including the polyploids, are shown on a single cladogram in Fig. 5.10. Here *P. mistassinica* is represented as a polymorphic lineage with at least three infraspecific taxa. *Primula incana* is allied to *P. alcalina* on the basis of biogeographic and morphological affinities, and *P. laurentiana* is allied to *P. mistassinica* for the same reasons. *P. stricta* is represented as a questionable hybrid of *P. incana* and *P. laurentiana* although as noted, it is equally probable that it is an allopolyploid of two European species, *P. scotica* and *P. scandinavica*.

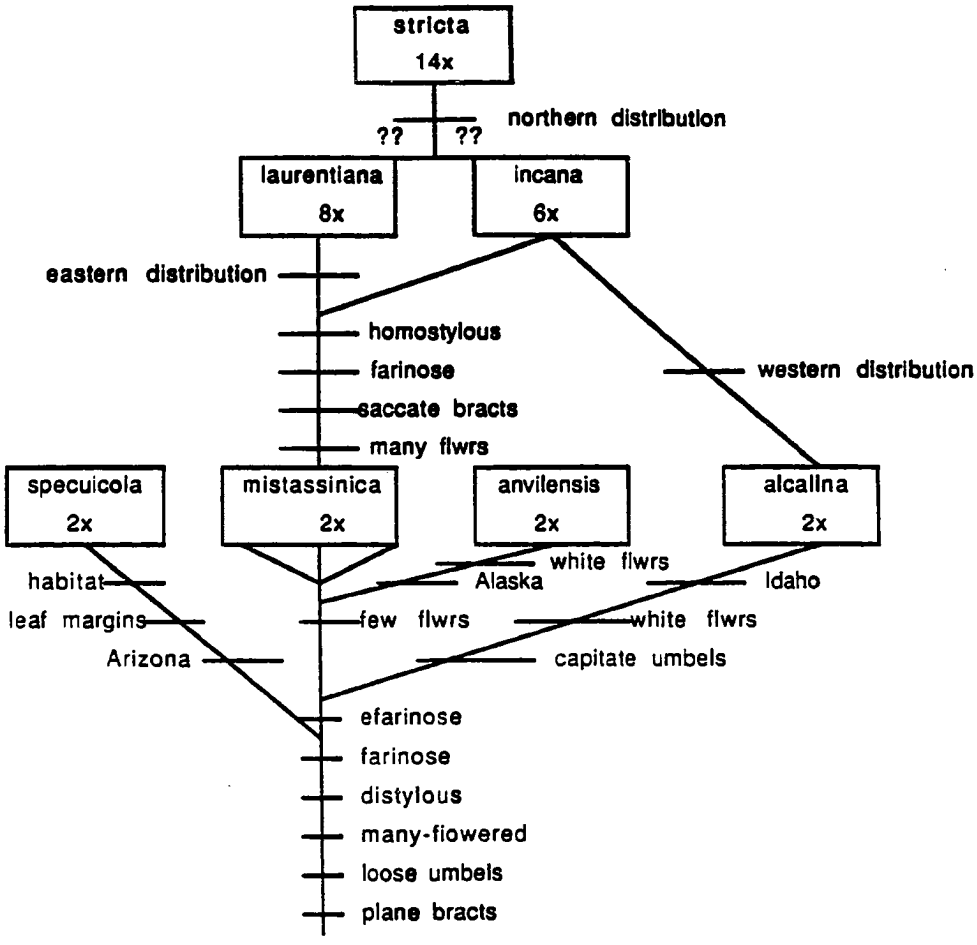


Fig. 5.10. Polyploid complex of species in sect. Aleuritia. Hybrids have character states derived from one or both parents.

Section *Armerina* Lindley.

Most of the members of section *Armerina* belong in the steppes and mountains of Central Asia. The sole circumpolar member is *P. nutans* Georgi (formerly called *P. sibirica* Jacq.), which in North America is found only in scattered populations in Alaska and the Yukon. A second member of the section, *P. egaliksensis* Wormskj., is found across arctic and boreal North America to Greenland, and rarely on the Asiatic side of the Bering Strait. Because only two taxa are involved, no cladistic analysis was done, but on the basis of several lines of evidence, I propose a hybrid background for *P. egaliksensis*, between *P. nutans* in section *Armerina*, and *P. mistassinica* or its ancestral form in section *Aleuritia*.

The wide distribution of the diploid distylous species *P. nutans* suggests it is a relatively old taxon. Mäkinen and Mäkinen (1964) have described how Pleistocene isolation may have created the Fennoscandian subspecies, *finnmarchia*, which differs only in its shorter corolla tube. Otherwise, specimens of subspecies *nutans* from Central Asia, northeastern Siberia, Alaska, and the Yukon are remarkably similar in morphology. The scattered populations of *P. nutans* that remain in Alaska, the Yukon, and Siberia are probably Pleistocene survivors where they persisted in boggy areas of unglaciated Beringia. If *P. nutans* once extended further east, it must have been extirpated there by at least the late Wisconsin ice sheets. It may be significant that *P. nutans* is the only arctic Primula with the capacity for vegetative reproduction. This ability may have enabled it to survive in spite of potentially disasterous Pleistocene and Holocene changes in the pollinator fauna.

Primula egaliksensis is a homostylous tetraploid with a close phenotypic resemblance to *P. nutans*, although it does not share the rhizomatous tendencies of that species. The resemblance is close enough for the general assumption to be made that *P. egaliksensis* is a derivative of *P. nutans* (Fernald 1928; Smith and Fletcher 1943), although until now no one has suggested the other parent. I agree that *Primula nutans* is almost certainly one of the progenitors of *P. egaliksensis*, and I propose here that the North American species *P. mistassinica* is the other. The evidence supporting this is morphological, cytological and biogeographical.

First, the chromosome number of *P. egaliksensis* ($2n = 36, 40$) indicates a hybrid background. Members of section *Armerina* are known to have a base number of 11 and *Primula nutans* is a diploid, $2n = 22$. Members of section *Aleuritia* have a base number of 9. *P. egaliksensis* could represent an

autopolyploid of *P. nutans* with a loss of four entire chromosomes, but an allopolyploid origin between a taxon with a base number of 11 and one with x = 9 is more likely: *P. nutans* at x =11 crossed with a diploid member of section *Aleuritia* to give a 4x number of $2n = 40$. The numerous counts of $2n = 36$ for *P. egaliksensis* suggest that aneuploidal reduction from $2n = 40$ has indeed occured. It is difficult to determine if both numbers exist, or if the higher counts are approximations.

The shared morphological features that led early authors to ally *P. egaliksensis* with *P. nutans* are the ovate pedicellate leaves and slender cylindrical capsules. A close inspection of these two species as well as of *P. mistassinica*, the only widespread diploid member of section *Aleuritia* in North America, indicates that *P. egaliksensis* is strikingly intermediate in its overall anatomy and morphology (Table 5.4). Leaves, bracts, glands, flowers, pollen, capsules, and seeds show characterics of both putative parents, with an overall tendency towards *P. nutans*. This tendency is to be expected since that species presumably contributed the larger proportion of the genome.

Table 5.4. Comparative morphology of *Primula nutans, P. egaliksensis,* and *P. mistassinica.*

	nutans	*egaliksensis*	*mistassinica*
farina	no	no	sometimes
leaf shape	ovate pedicellate	ovate pedicellate	spathulate
leaf margins	entire	entire to widely denticulate	denticulate
bract base	saccate, auriculate	saccate	plane
gland type	articulated hairs	articulated hairs & capitate	capitate
flower color	lilac	lilac, white	lilac, rarely white
distyly	yes	no	yes
pollen exine	widely reticulate	medium reticulate	microreticulate
# colpi	none	4	3
chromosome #	$2n = 22$	$2n = 36,40$	$2n = 18$
capsule shape	cylindrical	cylindrical	elliptical
seed color	light brown	light brown	medium brown

The morphological and cytological characteristics of *P. mistassinica* that suggest an ancestral relationship to *P. egaliksensis* are equally applicable to its Eurasiatic counterpart *P. farinosa*. However, on biogeographic grounds the North American species is a far more likely candidate. *Primula mistassinica* becomes very rare in northwestern North America where *P. nutans* appears and *P. egaliksensis* bridges the gap between the two species and extends considerably north of the limit of *P. mistassinica* (Fig. 5.11). It nowhere comes close to the range of *P. farinosa* in Europe or in Asia.

On the basis of this evidence, I suggest that *P. egaliksensis* represents a stable and well-differentiated segmental allopolyploid between *P. nutans* and *P. mistassinica*. The two parental species may have come into contact in northwestern North America early in the Pleistocene, and hybridized there. Subsequent glacial advances and retreats reduced *P. nutans* in Alaska and the Yukon to scattered relict populations, and *P. mistassinica* retreated to eastern refugia. Deglaciation made territory available for the new polyploid hybrid, which as a homostyle has the colonizing advantage of self-fertility not available to either of its distylous progenitors. *Primula egaliksensis* has since spread throughout the arctic and boreal regions of North America, reproductively isolated from either of its diploid parents through polyploidy, and has been able to cross both the Bering Strait and to Greenland. The southernmost disjunct locations in Colorado and Wyoming can either be interpreted as the result of long distance dispersal, or as relicts of a previously wider range. If, as Weber (1967) has suggested, the presence of arctic disjuncts in the Rocky Mountains are the remnants of late Pleistocene distributions, the origin of *P. egaliksensis* may well predate the last glacial episode.

IV. Conclusions.

Together, cladistic and biogeographic methods can make complementary contributions towards a reconstruction of phylogenetic history. Cladistic methods operate on the assumption that because characters define taxonomic boundaries, the careful scrutiny of selected characters can provide insight into how the discrete units we call taxa have originated. There can never be excessive character analysis in

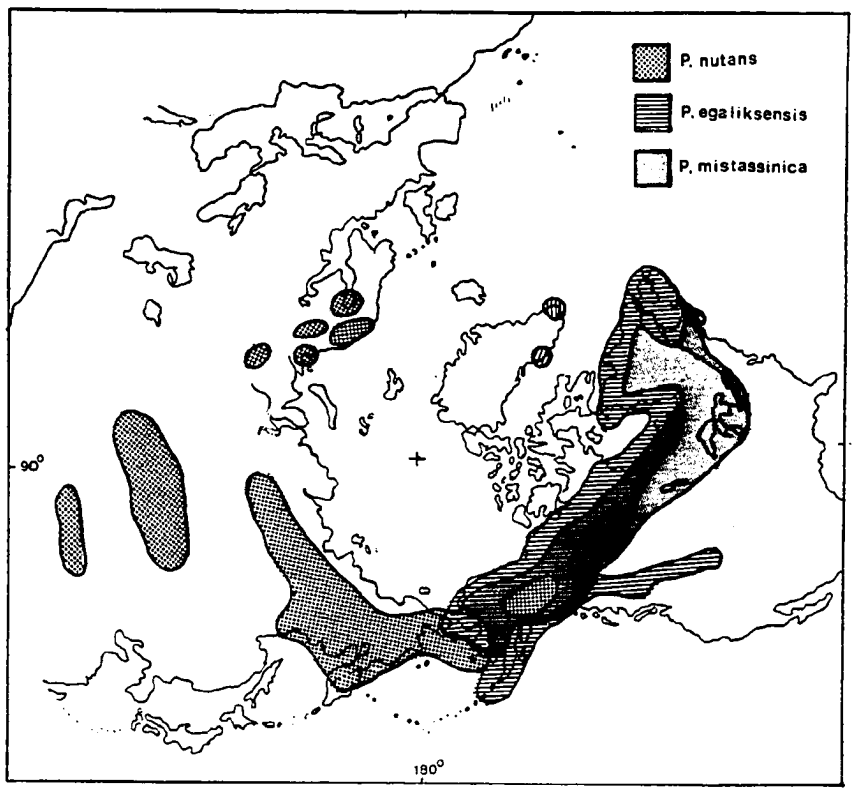


Fig. 5.11. Ranges of *Primula mistassinica*, *P. nutans*, and their putative hybrid, *P. egaliksensis*.

systematics, and to scrutinize how characters change is to scrutinize the mechanics of evolution. Cladistic analysis is selective vision, and any genus is the sum of many characters, not just the relatively few that can be polarized. True evolutionary relationships involve ecology, geography, and an unquantifiable overall gestalt that does not readily work into binary computer algorithms. At their best, cladistic reconstructions provide alternative evolutionary pathways for our critique. Historical biogeography can provide the landscape on which to place these alternatives.

Alone, descriptive biogeography has its own limitations. While it is easiest to depict and visualize vegetation in terms of modern analogues and as a unit defined by physiognomy and the dominance of certain genera, species do not act or react as a unit. The "boreal forest" and "tundra" of 20,000 years ago were in all probability quite different floristically than the boreal forest and tundra we see today, and their species do not necessarily have common histories. Plants disperse and adapt according to their unique genetic backgrounds and ecological requirements, and the history of a vegetation type can only be the generalized sum of the individual histories of its component taxa. For lack of alternative, we must base historical reconstructions on the assumption that the key to past behavior lies in what we observe in the present. However, it is with caution that phytogeographers treat the history of a vegetation type as equivalent to that of any taxon that is today a member of that association. Nevertheless, the generalized history of a unit such as the "boreal forest" or "tundra" provides a convenient reference for the separate, and probably highly complex, histories of its contemporary members.

For the genus ***Primula***, cladistic methods may eventually offer a great deal of potential for meaningful analysis at the sectional level, or within the Primulaceae, at the generic level. However, until more modern systematic work makes it possible to define taxonomic limits and character states of the Asiatic species and of some of the widespread and basic taxa like *P. farinosa*, the chief value of cladistic analysis may be that its preoccupation with character change enforces the question about what shared characters are, in evolutionary terms, the most important in this genus. The preceding analysis of sections *Cuneifolia, Crystallophlomis, Aleuritia,* and *Armerina* indicates that reversals, reticulate evolution, and multiple furcations may be a repeated pattern in *Primula*. In North America there is substantial paleogeographic and paleoecological information available. This provides a critical

background for the phylogenetic reconstruction of this genus. If as modern systematists we assume it is axiomatic that *all* lines of evidence must be taken into account to create taxonomic definitions, and if we desire, as we undoubtedly should, to attempt phylogenetic analysis, then we must apply all lines of evidence to a critique of our hypothetical reconstructions. Cladistics provides possibilities and biogeography provides the background to judge whether the possibilities are intuitively reasonable.

Chapter Six

Summary and Conclusions: migration and speciation in *Primula* as a model for the Alaskan flora.

The analysis and discussion provided in the work of such authors as Hultén (1937), Löve and Löve (1974), Murray (1981), Young (1971, 1982), and Yurtsev (1972, 1982) have given us the conception of an arctic flora with diverse origins. Some of its components may have developed in the Tertiary, some are probably remnants of a wider distribution disrupted by Quaternary events, some are probably recent migrants to the north, and some have evolved in situ. There has been a tendency to regard the arctic flora as a patchwork of smaller floristic groups such as the "arctic-alpine element", the "boreal element", or the "circumpolar element". These elements are defined only by overall ecology or geographic distribution, and are frequently discussed as if they had a common history. Yet, as I have commented earlier, the history of contemporary floristic associations is no more than the summed histories of its components. Therefore, I believe our next step towards understanding the complex origins and development of the arctic flora should be a focus on its individual taxa, to clarify their taxonomy, their ecology, their phytogeography, and the underlying processes that have led to their diversification. *Primula* provides an excellent model for just such an an analysis. Even though it is not a dominant genus nor even a particularly common one, I believe that understanding the biogeography and the modes of speciation here can give a valuable perspective on the origins of the modern Alaskan flora as whole. I suggest that the evolutionary processes that have created the *Primula* species we see today may well be widespread in the Beringian arctic, and that they have shaped the more widespread species in other genera that dominate the contemporary flora, as well as those restricted species we think of as unique representatives of far northern environments.

Biogeographic Affinities.

The strongest phytogeographical affinity that *Primula* shows is to Asia. *Primula nutans* and *P. tschuktschorum* have their closest relatives in the steppes and mountains of central Siberia. These appear in mountain chains and unglaciated

lowlands of the Altai in a northeastern arc past Lake Baikal, the Sea of Okhotsk, and eventually across Chukotka to Alaska. Another important line of migration and evolution, represented by *P. cuneifolia* and *P. borealis*, is a coastal route along the North Pacific from Japan through Kamtschatka to the Bering Sea region and across the Aleutian Islands. Again the movement has been strongly west to east.

There has been far less migration from the opposite hemisphere. The only species with an amphi-Atlantic connection, *P. stricta*, reaches its western extent in the Canadian Arctic. Whether *P. stricta* has European or American roots is problematical, and thus the question of overall migratory direction remains unanswered. However, it is clear that wherever the ultimate origin of *P. stricta* lies, the dispersal route has been a maritime one. Given sufficient time, there seems nothing to prevent *P. stricta* from eventually reaching northern Alaska via the Arctic Ocean coast line. In general, however, except for the widespread circumpolar species, the ties between the Alaskan flora and the European arctic flora are much weaker than those with Asia.

The Arctic may be a phytogeographic cross roads to some extent, but it contains a number of autochthonous species as well. Several of the *Primula* species found in Alaska have almost wholly American distributions, and *Primula anvilensis* is endemic to the northwestern part of the state. It is one of the very few Bering Strait taxa found only in North America. I have suggested that it originated in Alaska, a glacial isolate of the more widespread boreal species *P. mistassinica*. This latter species has a few representatives in Alaska, but they are probably recent eastern immigrants. *Primula egaliksensis* is another almost entirely North American species, at least in its distribution if not in its genetic heritage. One putative parent, *P. nutans*, is Eurasiatic; the other, *P. mistassinica*, is North American. If this species represents a hybrid contact between evolutionary lines from northeastern Asia and North America, its migration has been strongly to the east rather than to the west. The presence of *P. egaliksensis* as far east as Greenland and as far south as Colorado can be traced to dispersal routes along rivers and coastlines. One of the few species that appears to have moved north to the arctic from temperate North America is *P. incana*, whose affinities lie with the other members of section *Aleuritia* in the eastern forests and western plateaus. The distribution of *P. incana* follows the alkaline clay soils of the prairies and in the northern part of its range, in similar soil along river floodplains.

In Fig. 6.1, source regions and phytogeographic affinities for the Alaskan *Primula* species are shown. The strongest tie is to Asia: the central steppes, the eastern and northern mountains, and the Pacific coastal arc. There are also affinities to northern Europe, to temperate and boreal North America, and a core of native taxa as well. Various migration routes are represented: mountains, islands chains, coast lines, and along rivers. These are also the contemporary migration routes of birds, and dispersal may have been aided by avian agents. The timing of the arrival of these different *Primula* taxa may be as varied as their origins: a few may be relicts of a Tertiary flora, most quite likely have followed Quaternary ecological shifts, and some may be the product of very recent dispersal or speciation events.

Modes of speciation

Modern evolutionary theory has attempted to categorize the way species develop as one of several general models (cf. Grant 1971; Mayr 1970; Stebbins 1950; White 1978; Wiley 1981). The classical vicariance model of allopatric speciation proposes that a taxonomic group is physically divided by some event and the subgroups then develop separate lineages through the processes of geographic differentiation and local adaptation. These subgroups may be either two large populations, or a large population and a peripheral isolate. In parapatric speciation, two populations remain in narrow contact and may interbreed there, but still differentiate otherwise through local selection or stochastic processes. In stasipatric speciation (sensu White 1978) a major chromosomal rearrangement such as an inversion creates a genotype that is fully fertile in the homozygous state but either inviable or of lower fertility when heterozygous. Thus, a new lineage can develop from the ancestral species but does not require physical separation. A related model of sympatric speciation covers a number of other mechanisms leading to speciation without geographic separation. These processes can include ecological changes (e.g. pollinator shifts), hybridization, polyploidy, or apomixis, and presume that reproductive isolation in some degree drives the speciation process.

The northern primulas provide examples of several of these modes of speciation. *Primula anvilensis* appears to be a classic case of allopatric speciation,

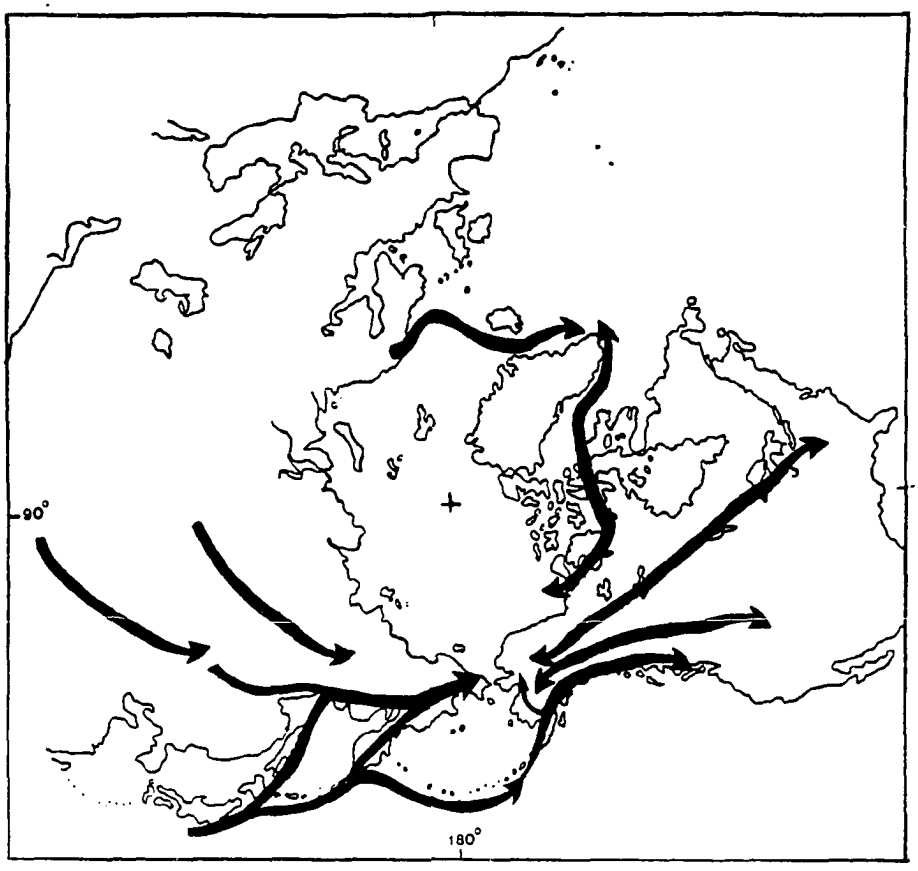


Fig. 6.1. Phytogeographic affinities and apparent migration routes for the Alaskan flora.

in which isolation plus local adaptation has created a separate lineage. Allopatric speciation may also explain the origin of *P. tschuktschorum* from its Asiatic relatives *P. xanthobasis* and *P. nivalis*, but their taxonomic and biogeographic relationships are not yet fully clarified. The origin of *P. cuneifolia* subsp. *saxifragifolia*, the homostylous derivative of subsp. *cuneifolia*, closely follows the model of parapatric speciation. While not yet differentiated at the species level, it seems reasonable to regard subsp. *saxifragifolia* as an incipient species. The two taxa are in contact across only a narrow zone in the western Aleutians. The development of the homostylous line can be attributed to a chance mutation plus local selective pressure for self-fertility. This same model can also be called upon to explain the origin of *P. eximia* from *P. tschuktschorum*, in which the homostylous line has differentiated sufficiently to be called a species. *Primula tschuktschorum* may originally have had only a narrow contact with *P. eximia* but today it is completely surrounded by its reproductively far more sucessful derivative.

Sympatric speciation can be the appropriate model for *Primula egaliksensis, P. incana*, and *P. borealis*. Certainly both hybridization and polyploidy are integral in the genetic background of *P. egaliksensis* and *P. incana*, and probably of *P. borealis* as well. The origin of *P. incana* is somewhat complex. According to the scenario suggested in Chapter 5, it initially involved separation, partial differentiation, and secondary contact resulting in allopolyploidy. Consequently, it may be more appropriate to invoke both the allopatric and sympatric models of speciation to account for the origin of *P. incana*.

Reproductive specialization is one of the strongest factors accounting for the ultimate diversity of *Primula* species in the arctic. Distyly and homostyly, i.e. obligate outcrossing and its restraints, and selfing and its opportunities, are the recurrent themes in this genus. These reproductive modes plus hybridization allied with polyploidy can enforce ecological specialization or make ecological generalization possible. They can restrict gene flow, or they can make dispersal and migration feasible. Polyploidy can protect against the detrimental effects of inbreeding and enable homostyles to pass through the temporary bottleneck of inbreeding depression. Homostyly with or without other genetic change can be a successful mutation when coupled with strong selective pressure for self-fertility and/or when the homostyle retains or develops the ability for facultative outcrossing.

Thus the success of the genus *Primula* can ultimately be attributed to its

reproductive strategies and to chance. Mutations to homostyly and mitotic or meiotic failure leading to polyploidy are initially stochastic events. Successful colonization depends on random dispersal and opportunity in available habitats. From these rare events, selective forces take over and undoubtedly in at least some arctic environments there is strong selection for the ability to self-fertilize. However, it is far too simplistic to treat selfing as a single-faceted reproductive strategy. *Primula* exemplifies the diverse possibilities for both outcrossing and inbreeding species. The arctic taxa show an entire spectrum of reproductive modes from obligate outcrossing to facultative selfing. They also demonstrate the diversity of genetic backgrounds that accompany these reproductive strategies and which can account for "success" of a taxon, whether it is measured in breadth of range, abundance, or longevity.

Conclusions.

There are several lessons to be learned from *Primula* relative to its role in the arctic flora. First, we must look in many directions for phytogeographic affinities. From Asia there are ties to the steppes, to the mountains, and to the Pacific coastal flora. On our continent, there are connections to the eastern boreal forest and to the western plains and plateaus. Our taxa are not only locally adapted immigrants, but also autochthonous species that have developed in a number of ways. Separation and isolation, chance mutations acted upon by selection, hybridization, and polyploidy have all played important roles. These factors can be influential in themselves, but for *Primula,* they have been particularly critical due to their effects on reproductive biology. In turn, the mode, timing, and strength of outcrossing or inbreeding have become driving forces in the evolution of the genus. This importance of reproductive biology for understanding diversity in the arctic flora may be the most valuable lesson to be learned from *Primula.*

While few other northern genera offer a focus as dramatic or well-studied as distyly, it is clear that there are other reproductive systems equally complex and equally instructive. Comparative studies on the reproductive biology of related arctic taxa has only just begun, but in this type of analysis may lie the keys to a new understanding of the roots of our flora and the evolutionary forces shaping it today.

APPENDIX 1. CHARACTERS USED IN THE PHENETIC ANALYSIS.

Key to Appendix 1

1. Mean flower number (n, sd)
2. Mean pedicel length (n, sd)
3. Mean corolla width (n, sd)
4. Mean corolla tube length (n, sd)
5. Mean calyx length (n, sd)
6. Mean leaf length (n, sd)
7. Mean leaf width (n, sd)
8. Mean scape height (n, sd)
9. Base number (0 = 9, 1 = 11, 2 = other)
10. Leaf pedicels (0 = distinct, 1 = obscure)
11. Leaf blade (0 = lanceolate, 1 = spathulate, 2 = elliptical-ovate, 3 = cuneate)
12. Leaf margins (0 = dentate, 1 = denticulate, 2 = entire, 3 = widely dentate)
13. Bract base (0 = plane, 1 = saccate, 2 = auriculate)
14. Bract shape (0 = involute, 1 = flat)
15. Pedicel type (0 = capillary, 1 = erect)
16. Inflorescence shape (0 = capitate umbel, 1 = loose umbel, 2 = not umbellate)
17. Calyx division (0 = <1/4, 1 = 1/4-1/2, 2 = >1/2)
18. Farina (0 = abundant, 1 = medium, 2 = absent)
19. Corolla color (0 = white, 1 = lilac, 2 = lilac or white, 3 = magenta, 4 = rose)
20. Corolla limb (0 = entire, 1 = cordate, 2 = deeply cleft)
21. Exine (0 = microreticulate, 1 = reticulate, 2 =broadly reticulate)
22. Colpi (0 = obscure, 1 = 3, 2 = > 3)
23. Capsule shape (0 = ovate, 1 = narrowly cylindrical, 2 = elliptical, 3 = broadly cylindrical)
24. Seed coat (0 = reticulate, 1 = vesiculate, 3 = reticulate/flanged)
25. Gland type (0 = capitate, 1 = capitate/articulate, 2= articulate only)
26. Corolla glands (0 = absent, 1 = present)
27. Corolla tube/calyx (0 = equal, 1 = exserted, 2 = strongly exserted)
28. Calyx ribs (0 = present, 1 = obscure)
29. Calyx color (0 = green-purple, 1 = green-black)
30. Calyx shape (0 = urceolate, 1 = campanulate, 2 = cylindrical)
31. Capsule/calyx (o = equal, 1 = exserted, 2 = strongly exserted)
32. Leaf texture (0 = fleshy, 1 = somewhat fleshy, 2 = thin, not fleshy)

APPENDIX 1

CHARACTER	TAXA			
	eximia	*tschuktschorum*	*cuneifolia*	*saxifragifolia*
1. Flower number	5.1 (63, 2.3)	1.6 (35, 0.7)	2.8 (44, 1.2)	2.1 (96, 1.3)
2. Pedicel length	7.5 (63, 4.9)	6.8 (34, 2.9)	6.8 (44, 4.2)	3.3 (95, 2.5)
3. Corolla width	6.1 (63, 3.6)	18.3 (34, 4.4)	20.9 (42, 4.4)	15.3 (83, 3.5)
4. Corolla tube length	11.7 (63, 1.8)	8.3 (34, 1.5)	8.4 (42, 2.1)	6.7 (94, 1.1)
5. Calyx length	5.9 (63, 1.1)	7.1 (34, 1.3)	4.9 (41, 1.1)	4.1 (82, 1.0)
6. Leaf length	50.5 (63, 20.4)	40.5 (34, 15.4)	47.1 (44, 16.8)	23.1 (84, 10.1)
7. Leaf width	8.6 (63, 3.2)	2.6 (34, 0.8)	10.0 (44, 3.4)	8.2 (95, 2.5)
8. Scape height	92.4 (63, 38.7)	65.0 (34, 18.9)	106.7 (44, 40.0)	34.9 (95, 24.4)
9. Base number	1	1	1	1
10. Leaf pedicels	1	1	1	1
11. Leaf blade	0	0	3	3
12. Leaf margins	3	3	0	0
13. Bract base	0	0	0	0
14. Bract shape	0	0	0	0
15. Pedicel type	1	0	0	1
16. Umbel shape	1	2	2	2
17. Calyx division	2	2	2	2
18. Farina	0	2	2	2
19. Corolla color	3	3	4	4
20. Corolla limb	0	0	2	2
21. Exine	0	0	0	0
22. Colpi	1	1	1	1
23. Capsule shape	3	3	0	0
24. Seed coat	1	1	2	2
25. Gland type	0	0	0	0
26.Corolla glands	0	0	1	1
27. Corolla tube/calyx	2	2	1	1
28. Calyx ribs	1	1	1	1
29. Calyx color	1	1	0	0
30. Calyx shape	2	2	0	0
31. Capsule/calyx	2	2	0	0
32. Leaf texture	0	0	1	1

APPENDIX 1 CONT.

CHARACTER	TAXA			
	alcalina	*anvilensis*	*mistassinica*	*specuicola*
1. Flower number	7.0 (11, 1.7)	3.1 (120, 2.0)	3.2 (135, 2.0)	12.0 (27, 5.6)
2. Pedicel length	3.1 (11, 1.5)	6.9 (120, 3.6)	9.9 (195, 12.4)	21.0 (26, 9.9)
3. Corolla width	9.1 (11, 1.0)	7.0 (118, 1.5)	10.9 (115, 1.8)	11.2 (20, 3.2)
4. Corolla tube length	4.9 (11, 0.7)	3.0 (118, 0.5)	6.1 (47, 1.3)	10.9 (22, 2.1)
5. Calyx length	4.9 (11, 0.7)	2.8 (120, 0.5)	5.2 (208, 1.5)	6.1 (27, 1.5)
6. Leaf length	20.1 (11, 6.7)	10.6 (120, 5.1)	17.8 (130, 9.4)	96.3 (27, 38.2)
7. Leaf width	6.1 (11, 2.2)	2.7 (120, 1.1)	5.1 (130, 2.0)	14.2 (27, 5.6)
8. Scape height	126.8 (11, 59.4)	56.6 (120, 21.8)	86.5 (209, 37.6)	151.7 (26, 49.8)
9. Base number	0	0	0	0
10. Leaf pedicels	1	1	1	1
11. Leaf blade	1	1	1	1
12. Leaf margins	1	1	1	1
13. Bract base	0	0	0	0
14. Bract shape	1	0	0	0
15. Pedicel type	0	0	0	0
16. Umbel shape	0	2	2	1
17. Calyx division	1	1	1	1
18. Farina	0	2	2	0
19. Corolla color	1	1	1	1
20. Corolla limb	0	0	1	1
21. Exine	1	1	1	1
22. Colpi	0	0	0	0
23. Capsule shape	2	2	2	2
24. Seed coat	0	0	0	0
25. Gland type	0	0	0	0
26. Corolla glands	0	0	0	0
27. Corolla tube/calyx	0	0	1	2
28. Calyx ribs	1	1	1	1
29. Calyx color	0	0	0	0
30. Calyx shape	1	1	1	1
31. Capsule/calyx	1	1	1	1
32. Leaf texture	2	2	2	2

APPENDIX 1 CONT.

CHARACTER	TAXA			
	borealis	*incana*	*laurentiana*	*stricta*
1. Flower number	4.2 (112, 1.9)	8.5 (107, 3.9)	5.1 (71, 2.3)	3.6 (72, 1.5)
2. Pedicel length	4.7 (102, 4.6)	5.4 (82, 3.9)	6.4 (45, 4.4)	3.1 (56, 1.4)
3. Corolla width	13.2 (101, 2.2)	5.2 (79, 1.9)	11.7 (37, 2.7)	6.2 (54, 1.5)
4. Corolla tube length	16.9 (103, 1.4)	6.2 (78, 1.2)	7.6 (37, 0.9)	6.3 (54, 0.9)
5. Calyx length	5.0 (112, 0.7)	5.6 (99, 1.3)	6.4 (89, 1.2)	5.0 (72, 0.8)
6. Leaf length	16.8 (12, 7.8)	42.7 (105, 16.3)	53.9 (89, 24.6)	20.8 (71, 10.2)
7. Leaf width	3.8 (112, 1.7)	7.9 (107, 3.2)	8.6 (89, 2.8)	4.7 (71, 2.3)
8. Scape height	45.8 (112, 20.9)	212.7 (107, 102.5)	183.2 (89, 79.4)	93.0 (72, 45.9)
9. Base number	0	0	0	0
10. Leaf pedicels	1	1	1	1
11. Leaf blade	1	1	1	1
12. Leaf margins	1	1	1	1
13. Bract base	1	1	1	1
14. Bract shape	0	1	0	0
15. Pedicel type	1	1	0	1
16. Umbel shape	1	0	0	2
17. Calyx division	1	0	1	1
18. Farina	1	0	0	0
19. Corolla color	1	1	1	1
20. Corolla limb	1	1	1	1
21. Exine	1	1	1	1
22. Colpi	1	2	2	2
23. Capsule shape	2	2	2	2
24. Seed coat	0	0	0	0
25. Gland type	0	0	0	0
26. Corolla glands	0	0	0	0
27. Corolla tube/calyx	1	1	1	1
28. Calyx ribs	1	1	1	1
29. Calyx color	0	0	0	0
30. Calyx shape	1	1	1	1
31. Capsule/calyx	1	1	1	0
32. Leaf texture	2	2	2	2

APPENDIX 1 CONT.

CHARACTER	TAXA	
	egaliksensis	*nutans*
1. Flower number	3.0 (84, 1.1)	2.2 (84, 0.9)
2. Pedicel length	6.1 (75, 4.0)	13.2 (82, 6.4)
3. Corolla width	4.9 (74, 1.6)	13.3 (82, 2.3)
4. Corolla tube length	5.9 (75, 0.9)	8.5 (81, 2.0)
5. Calyx length	4.6 (83, 0.8)	5.1 (81, 1.0)
6. Leaf length	23.8 (84, 11.1)	18.1 (66, 10.3)
7. Leaf width	5.4 (84, 2.3)	6.7 (67, 3.0)
8. Scape height	102.7 (84, 45.4)	101.5 (84, 50.5)
9. Base number	2	1
10. Leaf pedicels	0	0
11. Leaf blade	2	2
12. Leaf margins	2	2
13. Bract base	1	2
14. Bract shape	0	0
15. Pedicel type	0	0
16. Umbel shape	2	2
17. Calyx division	0	0
18. Farina	1	2
19. Corolla color	2	1
20. Corolla limb	1	1
21. Exine	1	2
22. Colpi	2	0
23. Capsule shape	1	1
24. Seed coat	0	0
25. Gland type	1	2
26. Corolla glands	0	0
27. Corolla tube/calyx	2	2
28. Calyx ribs	1	0
29. Calyx color	0	0
30. Calyx shape	2	2
31. Capsule/calyx	2	2
32. Leaf texture	2	2

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